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**ON THE CLASSIFICATION OF GENERALIZED COMPETITIVE
ATKINSON-ALLEN MODELS VIA THE DYNAMICS ON THE
BOUNDARY OF THE CARRYING SIMPLEX**

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ABSTRACT. We propose the generalized competitive Atkinson-Allen map

$$T_i(x) = \frac{(1+r_i)(1-c_i)x_i}{1 + \sum_{j=1}^n b_{ij}x_j} + c_i x_i, 0 < c_i < 1, b_{ij}, r_i > 0, i, j = 1, \dots, n,$$

which is the classical Atkinson-Allen map when $r_i = 1$ and $c_i = c$ for all $i = 1, \dots, n$ and a discretized system of the competitive Lotka-Volterra equations. It is proved that every n -dimensional map T of this form admits a carrying simplex Σ which is a globally attracting invariant hypersurface of codimension one. We define an equivalence relation relative to local stability of fixed points on the boundary of Σ on the space of all such three-dimensional maps. In the three-dimensional case we list a total of 33 stable equivalence classes and draw the corresponding phase portraits on each Σ . The dynamics of the generalized competitive Atkinson-Allen map differs from the dynamics of the standard one in that Neimark-Sacker bifurcations occur in two classes for which no such bifurcations were possible for the standard competitive Atkinson-Allen map. We also found Chenciner bifurcations by numerical examples which implies that two invariant closed curves can coexist for this model, whereas those have not yet been found for all other three-dimensional competitive mappings via the carrying simplex. In one class every map admits a heteroclinic cycle; we provide a stability criterion for heteroclinic cycles. Besides, the generalized Atkinson-Allen model is not dynamically consistent with the Lotka-Volterra system.

1. Introduction. By Hirsch's carrying simplex theory [26], it is known that every strongly competitive and dissipative system of Kolmogorov ODEs for which the origin is a repeller possesses a globally attracting invariant hypersurface Σ of codimension one. Furthermore, Σ is homeomorphic to the $(n-1)$ -dimensional standard probability simplex $\Delta^{n-1} = \{x \in \mathbb{R}_+^n : \sum_i x_i = 1\}$, such that every nontrivial orbit in the nonnegative cone \mathbb{R}_+^n is asymptotic to one in Σ . This result implies that n -dimensional strongly competitive continuous-time systems behave like general $(n-1)$ -dimensional systems, and hence the Poincaré-Bendixson theorem holds for the 3-dimensional case. Based on this remarkable theory, many researchers have obtained a lot of results on nontrivial dynamics for 3-dimensional continuous-time competitive systems, including the existence and multiplicity of limit cycles [22, 23, 24, 28, 34, 38, 47, 48, 52]; the existence of centers and heteroclinic cycles [8, 34, 52]; and ruling out periodic orbits [8, 34, 45, 52]. Moreover, the readers can consult [4, 6, 7, 29, 30, 39, 49, 50, 51] for the geometrical properties of carrying simplices and their impact on the dynamics.

The research on the existence of carrying simplex for discrete-time systems began with Smith's work [43] on the dynamical behavior of the Poincaré map induced by time-periodic competitive Kolmogorov ODEs. Based on the early work of Hirsch [26] and Smith [43], there have been many results on the existence of carrying simplex for competitive mappings; see [46, 12, 25, 42, 5, 33, 32]. We refer the readers to the most recent article [32] for a review of the development of carrying simplex theory for competitive mappings. In [32], Jiang and Niu provided a readily checked criterion that guarantees the existence of carrying simplex for the continuous map $T : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ of the type

$$T(x) = (T_1(x), \dots, T_n(x)) = (x_1 G_1(x), \dots, x_n G_n(x)), \quad (1)$$

where $G_i(x) > 0$, $i = 1, \dots, n$, for all $x \in \mathbb{R}_+^n$. They applied this criterion to show that all maps in a large family of competitive maps have a carrying simplex.

Their result enriches the existing literature on discrete-time competitive dynamical systems with carrying simplices.

The importance of the existence of carrying simplex Σ stems from the fact that Σ captures the relevant long-term dynamics. It contains all non-trivial fixed points, periodic orbits, invariant closed curves and heteroclinic cycles, etc. In order to analyze the global dynamics of such discrete-time systems, it suffices to investigate the dynamics on Σ . However, compared with the continuous-time competitive systems, the research in discrete-time competitive systems via carrying simplices is much less. In [42] Ruiz-Herrera provided an exclusion criterion for discrete-time competitive models of two or three species via carrying simplices. Jiang and Niu [31] deduced an index formula on the sum of the indices of all fixed points on Σ for the three-dimensional map T of type (1):

$$\sum_{\theta \in \mathcal{E}_v} \mathcal{J}(\theta, T) + 2 \sum_{\theta \in \mathcal{E}_s} \mathcal{J}(\theta, T) + 4 \sum_{\theta \in \mathcal{E}_p} \mathcal{J}(\theta, T) = 1. \quad (2)$$

Here $\mathcal{J}(\theta, T)$ stands for the index of T at the fixed point θ , and \mathcal{E}_v , \mathcal{E}_s , and \mathcal{E}_p are the sets of nontrivial axial, planar, and positive fixed points, respectively. Based on the index formula, an alternative classification for 3-dimensional ($n = 3$) Atkinson-Allen models

$$T_i(x) = \frac{2(1-c)x_i}{1 + \sum_{j=1}^n b_{ij}x_j} + cx_i, \quad 0 < c < 1, \quad b_{ij} > 0, \quad i, j = 1, \dots, n \quad (3)$$

was given in [31] and an alternative classification for 3-dimensional Leslie-Gower models was also given in [32]. Neimark-Sacker bifurcations were investigated within each class of these two types of models. Neimark-Sacker bifurcation is the birth of an invariant closed curve from a fixed point in discrete-time dynamical systems, and either all orbits are periodic, or all orbits are dense on the invariant closed curve. Such an invariant closed curve corresponds to either a subharmonic or a quasiperiodic solution in continuous-time systems. In [33], Jiang *et al.* studied the occurrence of heteroclinic cycles via carrying simplices for competitive maps (1) and provided their stability criteria.

In this paper, we study the long-term dynamics of the map

$$T_i(x) = \frac{(1+r_i)(1-c_i)x_i}{1 + \sum_{j=1}^n b_{ij}x_j} + c_i x_i, \quad 0 < c_i < 1, \quad b_{ij}, r_i > 0, \quad i, j = 1, \dots, n \quad (4)$$

defined on \mathbb{R}_+^n , which plays a role as a discrete-time Lotka-Volterra system. When $r_i = 1$ and $c_i = c$, the model induced by the map (4) reduces to the Atkinson-Allen model (3). Other generalizations of (3) considered by Roeger and Allen [41], Atkinson [2] and Allen *et al.* [1] are also special cases of (4). We call the model induced by (4) the *generalized Atkinson-Allen model*. Smith [44] analyzed a related two-dimensional discrete-time model for competition between populations of cyst-nematodes, due to Jones and Perry [35]. Similar models are also treated in the monograph [40]. He showed that it generates a monotone map in \mathbb{R}_+^2 . For the analysis of a special case of three-dimensional model (4), we refer the readers to [41, 12, 31]. Our principal aim is to investigate whether the discrete-time model (4) admits a carrying simplex such that one can study its long-term dynamics via the carrying simplex as studying the continuous-time competitive systems.

The derivation of discrete-time population models from first principles is notoriously difficult and mistakes are frequently made. In particular, a straightforward discretization of an established continuous-time model almost inevitably leads to

equations void of biological content ([21, 16]). We therefore give a mechanistic derivation of the model induced by the map (4).

We assume that the season is divided into three periods: one of competition, one of reproduction and one of survival. During the first period, the individuals of n species do not die, but compete for n different resources S_j . Assuming chemostat dynamics of the resources and a Holling type I functional response, we obtain the following equations for the resource dynamics:

$$\frac{dS_i}{dt} = D_i(\bar{S}_i - S_i) - S_i \sum_{j=1}^n a_{ij}x_j. \quad (5)$$

Assuming the resource dynamics is fast, the resource concentrations will have reached the following steady state by the end of the period of competition:

$$S_i = \frac{\bar{S}_i}{1 + \sum_{j=1}^n \frac{a_{ij}}{D_i} x_j}. \quad (6)$$

During the period of reproduction, individuals of species i will use only the resource S_i given by (6) to produce offspring (with a conversion factor γ_i) born at the beginning of the next period of competition. The adults of species i survive to the next period of competition with probability c_i . Putting all these assumptions together, we finally arrive at the following map T taking the state of the community at the beginning of one period of competition to the next one:

$$T_i(x) = \frac{\gamma_i \bar{S}_i x_i}{1 + \sum_{j=1}^n \frac{a_{ij}}{D_i} x_j} + c_i x_i, \quad (7)$$

which is, of course, exactly the map (4), but with the parameters denoted in a different way. We shall keep the parameters of (4) to make comparison with the similar models treated in the papers mentioned above easier.

The generalized Atkinson-Allen model (4) can also be derived from the classical continuous-time competitive Lotka-Volterra (LV) system

$$\frac{dx_i(t)}{dt} = x_i(t) \left(\nu_i - \sum_{j=1}^n \mu_{ij} x_j(t) \right), \quad \nu_i, \mu_{ij} > 0, i, j = 1, \dots, n, \quad (8)$$

by using discretization scheme. Set $r_i = \frac{\nu_i}{1-c_i}$, $b_{ij} = \frac{\mu_{ij}}{1-c_i}$, where $0 < c_i < 1$. System (8) can be written as

$$\begin{aligned} \frac{dx_i(t)}{dt} &= (1 - c_i)x_i(t)(r_i - \sum_{j=1}^n b_{ij}x_j(t)) \\ &= r_i(1 - c_i)x_i(t) + c_i x_i(t) \sum_{j=1}^n b_{ij}x_j(t) - x_i(t) \sum_{j=1}^n b_{ij}x_j(t). \end{aligned} \quad (9)$$

By substituting $(x_i(t+h) - x_i(t))/h$ for $dx_i(t)/dt$ and using a mixed implicit-explicit approximation we derive

$$\begin{aligned} \frac{x_i(t+h) - x_i(t)}{h} &= r_i(1 - c_i)x_i(t) + c_i x_i(t) \sum_{j=1}^n b_{ij}x_j(t) \\ &\quad - x_i(t+h) \sum_{j=1}^n b_{ij}x_j(t), \end{aligned} \quad (10)$$

which can be expressed more simply as

$$x_i(t+h) = \frac{(1 + hr_i)(1 - c_i)x_i(t)}{1 + h \sum_{j=1}^n b_{ij}x_j(t)} + c_i x_i(t).$$

Set $h = 1$. Then we obtain the discrete-time generalized Atkinson-Allen system

$$x_i(t+1) = \frac{(1+r_i)(1-c_i)x_i(t)}{1 + \sum_{j=1}^n b_{ij}x_j(t)} + c_i x_i(t), \quad t = 0, 1, 2, \dots$$

Based on the criterion to guarantee the existence of carrying simplex provided by Jiang and Niu [32], we can prove that any n -dimensional model (4) possesses a carrying simplex. The long-term dynamics of (4) is studied further via the carrying simplex. We define an equivalence relation on the space of all three-dimensional models (4) which is similar to the one for the standard Atkinson-Allen models [31] and Leslie-Gower models [32]. Two models (4) are said to be equivalent relative to $\partial\Sigma$ (the boundary of Σ) if their boundary fixed points have the same locally dynamical property on Σ after a permutation of the indices $\{1, 2, 3\}$. We classify all three-dimensional generalized Atkinson-Allen models (4) by this equivalence relation using the index formula (2), and derive a total of 33 stable equivalence classes in terms of simple inequalities on the parameters c_i , r_i and b_{ij} . Then one can investigate the qualitative properties of the orbits, bifurcations and the occurrence of heteroclinic cycles within each class.

Eighteen classes (classes 1 to 18) which do not possess a positive fixed point have trivial dynamics, i.e., every nontrivial orbit converges to some fixed point on $\partial\Sigma$. The other 15 classes all have a unique positive fixed point which may contain much more complex dynamics. We prove that Neimark-Sacker bifurcations do not occur in classes 19 – 25 and class 32 while they do occur in classes 26 – 31. We construct examples in classes 26 – 29 and 31 which admit supercritical Neimark-Sacker bifurcations, so these classes can have stable invariant closed curves on Σ . Class 30 can admit subcritical Neimark-Sacker bifurcations, so this class can admit unstable invariant closed curves on Σ . However, Neimark-Sacker bifurcations can not occur in classes 28 and 30 for the three-dimensional standard Atkinson-Allen model (3). We also provided numerical examples in classes 26 – 29 which admit Chenciner bifurcations. The Chenciner bifurcation is a two-parameter bifurcation phenomenon of a fixed point, which can bifurcate two invariant closed curves simultaneously. So classes 26 – 29 can possess two invariant closed curves on Σ , which are first found in competitive mappings via carrying simplices. Specifically, we find that a large unstable invariant closed curve surrounding a small stable invariant closed curve can occur on Σ in classes 26, 28 and 29, while a stable fixed point and a stable invariant closed curve, separated by an unstable invariant closed curve can coexist on Σ in class 27. Numerical simulations show that two attracting invariant closed curves can coexist on Σ for some maps in class 29 (see Fig. 8), which is also found in competitive mappings via the carrying simplex for the first time. Via the carrying simplex, we show that each map in class 27 has a heteroclinic cycle, i.e. a cyclic arrangement of saddle fixed points and heteroclinic connections. We further provide the stability criteria on heteroclinic cycles. This cyclical fluctuation phenomenon has also been found in many other models; see Cushing [10], Davydova *et al.* [11] and Jiang *et al.* [33]. Moreover, it is shown that the generalized Atkinson-Allen model (4) is not dynamically consistent with the continuous-time competitive LV system (8). Our works will make it possible to study various interesting dynamics within each of classes 19 – 33 further.

The paper is organized as follows. Section 2 presents some notations and preliminaries. In Section 3, it is shown that any n -dimensional generalized Atkinson-Allen model admits a carrying simplex. The formula on the sum of all indices of fixed

points on Σ for three-dimensional models is reviewed. In Section 4, we define an equivalence relation on the space of all three-dimensional generalized Atkinson-Allen models and derive a total of 33 stable equivalence classes. The 33 stable equivalence classes with their corresponding phase portraits on Σ in terms of simple inequalities on the parameters are listed in Table 1 in the appendix. Furthermore, the dynamics on Σ of each class is studied. In Section 5, we compare the similarities and differences in the generalized Atkinson-Allen model and the Lotka-Volterra system numerically. The paper ends with a discussion in Section 6, where we list a few open problems for future investigation.

2. Notation and preliminaries. Throughout this paper, we reserve the symbol n for the dimension of the euclidean space \mathbb{R}^n and the symbol N for the set $\{1, \dots, n\}$. We denote the standard basis for \mathbb{R}^n by $\{e_{\{1\}}, \dots, e_{\{n\}}\}$. We use \mathbb{R}_+^n to denote the nonnegative cone $\{x \in \mathbb{R}^n : x_i \geq 0, \forall i \in N\}$. The interior of \mathbb{R}_+^n is the open cone $\dot{\mathbb{R}}_+^n := \{x \in \mathbb{R}_+^n : x_i > 0, \forall i \in N\}$ and the boundary of \mathbb{R}_+^n is $\partial\mathbb{R}_+^n := \mathbb{R}_+^n \setminus \dot{\mathbb{R}}_+^n$. We write \mathbb{Z}_+ for the set of nonnegative integers. We denote by $\mathbb{H}_{\{i\}}^+$ the i th positive coordinate axis and by $\pi_i = \{x \in \mathbb{R}_+^n : x_i = 0\}$ the i th coordinate plane. The symbol 0 stands for both the origin of \mathbb{R}^n and the real number 0.

Given two points x, z in \mathbb{R}^n , we write $x \leq z$ if $z - x \in \mathbb{R}_+^n$, $x < z$ if $z - x \in \mathbb{R}_+^n \setminus \{0\}$, and $x \ll z$ if $z - x \in \dot{\mathbb{R}}_+^n$. The reverse relations are denoted by $\geq, >, \gg$, respectively.

Let $X \subset \mathbb{R}^n$ and let $T : X \rightarrow X$ be a map. The positive orbit (trajectory) emanating from $y \in X$ is the set $\{y(j) : j \in \mathbb{Z}_+\}$, where $y(j) = T^j(y)$ and $y(0) = y$. A set $V \subset X$ is positively invariant under T , if $T(V) \subset V$ and invariant if $T(V) = V$. A fixed point y of T is a point $y \in X$ such that $T(y) = y$. We call $z \in X$ a k -periodic point of T if there exists some positive integer $k > 1$, such that $T^k(z) = z$ and $T^m(z) \neq z$ for every positive integer $m < k$. The k -periodic orbit of the k -periodic point z , $\{z, z(1), z(2), \dots, z(k-1)\}$, is often called a periodic orbit for short. A quasiperiodic curve is an invariant simple closed curve with every orbit being dense. For a differentiable map T , we let $DT(y)$ denote the Jacobian matrix of T at the point y .

Given a $k \times k$ matrix A , we write $A \geq 0$ if A is a nonnegative matrix (i.e., all its entries are nonnegative) and $A > 0$ if A is a positive matrix (i.e., all its entries are positive). The spectral radius of A , denoted by $\rho(A)$, is defined to be the maximum of the absolute values of its eigenvalues. Given $\emptyset \neq J \subseteq N$, we denote by A_J the submatrix of A with rows and columns from J . We use I to denote both the identity matrix and the identity mapping.

A map $T : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is competitive (or retrotone) in a subset $W \subset \mathbb{R}_+^n$ if for all $x, z \in W$ with $Tx < Tz$ one has that $x_i < z_i$ provided $z_i > 0$.

A *carrying simplex* for the map T is a subset Σ of $\mathbb{R}_+^n \setminus \{0\}$ with the following properties:

- (P1) Σ is compact and unordered;
- (P2) Σ is homeomorphic via radial projection to the $(n-1)$ -dimensional standard probability simplex $\Delta^{n-1} = \{x \in \mathbb{R}_+^n : \sum_i x_i = 1\}$;
- (P3) $\forall x \in \mathbb{R}_+^n \setminus \{0\}$, there is some $z \in \Sigma$ such that $\lim_{j \rightarrow \infty} |T^j x - T^j z| = 0$;
- (P4) $T(\Sigma) = \Sigma$, and $T : \Sigma \rightarrow \Sigma$ is a homeomorphism.

We denote the boundary of the carrying simplex Σ relative to \mathbb{R}_+^n by $\partial\Sigma = \Sigma \cap \partial\mathbb{R}_+^n$ and the interior of Σ relative to \mathbb{R}_+^n by $\dot{\Sigma} = \Sigma \setminus \partial\Sigma$.

We denote the set of all maps taking \mathbb{R}_+^n into itself by $\mathcal{T}(\mathbb{R}_+^n)$ and the set of all generalized competitive Atkinson-Allen maps on \mathbb{R}_+^n by $\text{CGAA}(n)$. In symbols:

$$\text{CGAA}(n) := \{T \in \mathcal{T}(\mathbb{R}_+^n) : T_i(x) = \frac{(1+r_i)(1-c_i)x_i}{1 + \sum_{j=1}^n b_{ij}x_j} + c_i x_i, 0 < c_i < 1, b_{ij}, r_i > 0, i, j \in N\}.$$

The competitiveness of each map in $\text{CGAA}(n)$ will be clear in §3.1. Finally we let B denote the $n \times n$ matrix with entries b_{ij} .

3. Carrying simplex and index theory. From now on we assume that $T(x) = (x_1 G_1(x), \dots, x_n G_n(x)) : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is a C^1 map with $G_i(x) > 0$ for all $x \in \mathbb{R}_+^n$. Note that this implies that $T_i(x) > 0$ if and only if $x_i > 0$ and, in particular, that $T^{-1}(\{0\}) = \{0\}$.

3.1. The existence of the carrying simplex. We first restate a criterion provided in [32] on the existence of carrying simplex for the map T .

Theorem 3.1 (Existence Criterion of Carrying Simplex [32]). *Suppose that*

- A1) $\partial G_i(x)/\partial x_j < 0$ for all $x \in \mathbb{R}_+^n$ and $i, j \in N$;
- A2) $\forall i \in N$, $T|_{\mathbb{H}_{\{i\}}^+} : \mathbb{H}_{\{i\}}^+ \rightarrow \mathbb{H}_{\{i\}}^+$ has a fixed point $q_{\{i\}} = q_i e_{\{i\}}$ with $q_i > 0$;
- A3) $\forall x \in [0, q] \setminus \{0\}$, $G_i(x) + \sum_{j \in \kappa(x)} x_j \frac{\partial G_i(x)}{\partial x_j} > 0$ for all $i \in \kappa(x)$ (or $G_i(x) + \sum_{j \in \kappa(x)} x_j \frac{\partial G_i(x)}{\partial x_j} > 0$ for all $i \in \kappa(x)$), where $\kappa(x) = \{j : x_j > 0\}$ is the support of x and $q = \sum q_{\{i\}} = (q_1, \dots, q_n)$.

Then T possesses a carrying simplex Σ .

Conditions A1) and A3) imply that T is competitive and also one-to-one in $[0, q]$. Specifically, A3) implies that $\det DT(x) > 0$ for all $x \in [0, q]$, and together with A1) it guarantees $(DT(x)_{\kappa(x)})^{-1} > 0$ for all $x \in [0, q] \setminus \{0\}$ by the proof of Theorem 3.1 in [32]. Then Proposition 4.1 in [42] ensures that T is competitive and one-to-one in $[0, q]$. Condition A1) also means that $G_i(y) < G_i(x)$ for all $i \in N$ provided $x < y$. This follows from

$$G_i(y) - G_i(x) = \int_0^1 DG_i(x_s)(y - x) ds,$$

where $x_s = x + s(y - x)$ with $s \in [0, 1]$. Thus, together with A2), A1) implies $G_i(0) > G_i(q_{\{i\}}) = 1$ for all $i \in N$, so 0 is a hyperbolic repeller for T . All non-trivial fixed points, periodic points and invariant closed curves lie on Σ .

Proposition 1. *Every map $T \in \text{CGAA}(n)$ admits a carrying simplex Σ .*

Proof. Set $G_i(x) = \frac{(1+r_i)(1-c_i)}{1 + \sum_j b_{ij}x_j} + c_i$, $i = 1, \dots, n$. Then we can write $T_i(x) = x_i G_i(x)$, $i = 1, \dots, n$. Since $G_i(x) > 0$ and $\partial G_i(x)/\partial x_j = -b_{ij} \frac{(G_i(x)-c_i)^2}{(1+r_i)(1-c_i)} < 0$, $\forall x \in \mathbb{R}_+^n$ and $i, j = 1, \dots, n$, A1) in Theorem 3.1 holds. Clearly, $q_{\{i\}} = \frac{r_i}{b_{ii}} e_{\{i\}}$ is a fixed point of $T|_{\mathbb{H}_{\{i\}}^+}$, i.e., A2) in Theorem 3.1 holds. Finally, for any $x \in \mathbb{R}_+^n$,

$$\begin{aligned} & G_i(x) + \sum_{j=1}^n x_j \frac{\partial G_i(x)}{\partial x_j} \\ &= G_i(x) - \sum_{j=1}^n x_j b_{ij} \frac{(G_i(x)-c_i)^2}{(1+r_i)(1-c_i)} \\ &= \frac{(G_i(x)-c_i)^2}{(1+r_i)(1-c_i)} + c_i > 0, \end{aligned}$$

so A3) in Theorem 3.1 also holds. The result now follows from Theorem 3.1. \square

Remark 1. Recall that when $r_i = 1$ and $c_i = c$, $i = 1, \dots, n$, the map $T \in \text{CGAA}(n)$ is the standard Atkinson-Allen map (see [41, 12, 31])

$$T : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n, \quad T_i(x) = \frac{2(1-c)x_i}{1 + \sum_j b_{ij}x_j} + cx_i, \quad 0 < c < 1, \quad b_{ij} > 0.$$

So Proposition 1 also implies that every Atkinson-Allen map admits a carrying simplex Σ , while this result was proved only for the three-dimensional case in [12].

Remark 2. Each map $T \in \text{CGAA}(n)$ is competitive and one-to-one on \mathbb{R}_+^n . Specifically, to show the injectivity of T we employ Lemma 3.4 in [9, p. 27], which says that if T is a continuous, locally homeomorphic map on a connected metric space for which the inverse image of every compact set is compact, then the cardinal number of the inverse image of every point is finite and the same for all points. Since, as noticed above, in our case $T^{-1}(\{0\}) = \{0\}$, this constant is one and hence T is one-to-one if T satisfies the above mentioned properties. Recall that A3) in Theorem 3.1 holds at every $x \in \mathbb{R}_+^n \setminus \{0\}$ for each $T \in \text{CGAA}(n)$, which implies that $\det DT(x) > 0$ for all $x \in \mathbb{R}_+^n$ (see the proof of Theorem 3.1 in [32]), so T is locally homeomorphic on \mathbb{R}_+^n . The injectivity of T will now follow once we have showed that the inverse image of every compact set is compact. To end this, let $W \subseteq T(\mathbb{R}_+^n)$ be a compact set in $T(\mathbb{R}_+^n)$. Because T is continuous, $T^{-1}(W)$ is a closed set in \mathbb{R}_+^n . Next we show that $T^{-1}(W)$ is bounded. If this was not the case, there would exist a sequence $x^k \in T^{-1}(W)$, such that $x_i^k \rightarrow +\infty$ as $k \rightarrow +\infty$ for at least one $i \in N$. Then by (4), one would have $T_i(x^k) \rightarrow +\infty$ as $k \rightarrow +\infty$, which would contradict the compactness of W . On the other hand, together with A1) in Theorem 3.1, A3) implies that $(DT(x)_{\kappa(x)})^{-1} > 0$ holds at every $x \in \mathbb{R}_+^n \setminus \{0\}$. It then follows from Proposition 4.1 in [42] that T is competitive on \mathbb{R}_+^n .

3.2. The index formula on the carrying simplex. Let $Q = I - T$ and $F = -Q = T - I$. Let x be a fixed point of T , that is, a zero of Q and F . The index of T at x is denoted by $\mathcal{J}(x, T)$ and the index of Q and F at x is denoted by $\mathcal{X}(x, Q)$ and $\mathcal{X}(x, F)$, respectively. The index $\mathcal{X}(x, Q)$ is defined as the sign of $\det DQ(x)$ if $\det DQ(x) \neq 0$, and the index $\mathcal{J}(x, T)$ as $\mathcal{X}(x, Q)$. If $\det DF(x) \neq 0$, we have

$$\mathcal{J}(x, T) = \mathcal{X}(x, -F) = (-1)^n \text{sgn}(\det DF(x)) = (-1)^n \mathcal{X}(x, F).$$

Assume $n = 3$. We call the fixed point x of the map $T : \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$ an *axial* fixed point if it lies on some coordinate axis; a *planar* fixed point if it lies in the interior of some coordinate plane; and a *positive* fixed point if it lies in $\mathring{\mathbb{R}}_+^3$. We denote the set of all nontrivial axial, planar, and positive fixed points by \mathcal{E}_v , \mathcal{E}_s , and \mathcal{E}_p , respectively.

Theorem 3.2 ([31]). *Suppose that $T(x) = (x_1 G_1(x), x_2 G_2(x), x_3 G_3(x)) : \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$ satisfies $\partial G_i / \partial x_j < 0$ for all $x \in \mathbb{R}_+^3$. Assume further that T possesses a carrying simplex Σ and that the continuous-time system $\dot{x} = F(x) = T(x) - x$ is dissipative with the origin 0 being a repeller. If T has only finitely many fixed points on Σ and 1 is not an eigenvalue of any of their Jacobian matrices, then*

$$\sum_{\theta \in \mathcal{E}_v} \mathcal{J}(\theta, T) + 2 \sum_{\theta \in \mathcal{E}_s} \mathcal{J}(\theta, T) + 4 \sum_{\theta \in \mathcal{E}_p} \mathcal{J}(\theta, T) = 1.$$

Now we consider the map $T \in \text{CGAA}(3)$. Suppose that all fixed points of T are isolated. T has three axial fixed points $q_{\{1\}} = (r_1/b_{11}, 0, 0)$, $q_{\{2\}} = (0, r_2/b_{22}, 0)$,

$q_{\{3\}} = (0, 0, r_3/b_{33})$. In the interior of π_i , there may exist a planar fixed point $v_{\{i\}}$ satisfying

$$b_{jj}x_j + b_{ji}x_i + b_{jk}x_k = r_j, \quad x_i = 0, \quad j \neq k \neq i. \quad (11)$$

T may also have a positive fixed point p in \mathbb{R}_+^3 which satisfies

$$b_{i1}x_1 + b_{i2}x_2 + b_{i3}x_3 = r_i, \quad i = 1, 2, 3. \quad (12)$$

We set $\mathcal{J}(v_{\{i\}}, T) = 0$ if there is no planar fixed point $v_{\{i\}}$ and $\mathcal{J}(p, T) = 0$ if there is no positive fixed point p .

It is easy to check that for $T \in \text{CGAA}(3)$, the conditions in Theorem 3.2 hold, so the following corollary is immediate from the above analysis and Theorem 3.2.

Corollary 1. *Assume that $T \in \text{CGAA}(3)$ and 1 is not an eigenvalue of any of the Jacobian matrices at the fixed points on Σ . Then we have*

$$\sum_{i=1}^3 (\mathcal{J}(q_{\{i\}}, T) + 2\mathcal{J}(v_{\{i\}}, T)) + 4\mathcal{J}(p, T) = 1.$$

Remark 3. Let $T \in \text{CGAA}(n)$. If T possesses a unique positive fixed point $p = (p_1, \dots, p_n)$, i.e.,

$$(Bx^\tau)_i = r_i, \quad i = 1, \dots, n \quad (13)$$

has a unique positive solution, then 1 is not an eigenvalue of

$$DT(p) = I - \text{diag}[p_i \frac{1-c_i}{1+r_i}]B,$$

where $\text{diag}[p_i \frac{1-c_i}{1+r_i}]$ denotes the diagonal matrix with the diagonal entries $p_i \frac{1-c_i}{1+r_i}$. Otherwise, 0 is an eigenvalue of the matrix $\text{diag}[p_i \frac{1-c_i}{1+r_i}]B$, and hence $\det B = 0$. Then (13) has either infinitely many solutions or no solution, a contradiction. By $(Bp^\tau)_i = r_i$, the sum of the entries of the i th row of the positive matrix $M := \text{diag}[\frac{1-c_i}{1+r_i}]B\text{diag}[p_i]$ is $(1-c_i)\frac{r_i}{1+r_i} < 1$. Then by Perron-Frobenius theorem, $0 < \rho(M) < 1$ is an eigenvalue of M and the magnitudes of the other eigenvalues are all less than 1. Set $\lambda^* := 1 - \rho(M)$. Since $\text{diag}[p_i \frac{1-c_i}{1+r_i}]B$ and M have the same eigenvalues, $0 < \lambda^* < 1$ is a real eigenvalue of $DT(p)$ whose associated eigenvector is strictly positive and all the other eigenvalues have real parts greater than 0 and less than 2.

4. The dynamics of the 3-dimensional generalized Atkinson-Allen model.

In this section, we analyze the long-term behavior of the map $T \in \text{CGAA}(3)$:

$$T_i(x) = \frac{(1+r_i)(1-c_i)x_i}{1+b_{i1}x_1+b_{i2}x_2+b_{i3}x_3} + c_i x_i, \quad i = 1, 2, 3. \quad (14)$$

It follows from Proposition 1 that T admits a 2-dimensional carrying simplex Σ homeomorphic to Δ^2 . Each coordinate plane π_i is invariant under T , and the restriction of T to π_i is a 2-dimensional map $T|_{\pi_i} \in \text{CGAA}(2)$, which has a one-dimensional carrying simplex, so $\partial\Sigma$ is composed of the one-dimensional carrying simplices of $T|_{\pi_i}$. Therefore, it is convenient for us to study the two-dimensional generalized Atkinson-Allen model first. We show that there are only four dynamical outcomes for two-dimensional cases. For $T \in \text{CGAA}(1)$, i.e., $T(x) = \frac{(1+r)(1-c)x}{1+bx} + cx$, the fixed point $p = r/b$ is the carrying simplex, i.e., p is globally asymptotically stable in \mathbb{R}_+ . This can be seen immediately but it also follows as a very special case of Proposition 1.

4.1. Classification of the 2-dimensional maps. In this subsection, we study the model $T \in \text{CGAA}(2)$:

$$T : (x_1, x_2) \mapsto \left(\frac{(1+r_1)(1-c_1)x_1}{1+b_{11}x_1+b_{12}x_2} + c_1x_1, \frac{(1+r_2)(1-c_2)x_2}{1+b_{21}x_1+b_{22}x_2} + c_2x_2 \right). \quad (15)$$

By Proposition 1, T admits a one-dimensional carrying simplex Σ homeomorphic to the line segment joining the two points $(0, 1)$ and $(1, 0)$.

Our first result (Proposition 2 below) says that every nontrivial trajectory of a two-dimensional generalized Atkinson-Allen map converges to a fixed point on the carrying simplex. To prove this, we need the following lemma which is a direct consequence of Corollary 4.4 in [44] adapted to maps on \mathbb{R}_+^2 .

Lemma 4.1. *Assume that the map $T : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ satisfies the following conditions:*

- (i) T is C^1 ,
- (ii) $\det DT(x) > 0$ for all $x \in \mathbb{R}_+^2$,
- (iii) the diagonal entries of $DT(x)$ are nonnegative and its off-diagonal entries are nonpositive,
- (iv) T is injective.

Then every orbit with compact closure in \mathbb{R}_+^2 converges to a fixed point of T .

Proposition 2. *Every nontrivial trajectory of $T \in \text{CGAA}(2)$ in \mathbb{R}_+^2 converges to a fixed point on Σ .*

Proof. The Jacobian matrix

$$DT(x) = \begin{pmatrix} \frac{(1+r_1)(1-c_1)(b_{12}x_2+1)}{(b_{11}x_1+b_{12}x_2+1)^2} + c_1 & -\frac{(1+r_1)(1-c_1)x_1b_{12}}{(b_{11}x_1+b_{12}x_2+1)^2} \\ -\frac{(1+r_2)(1-c_2)x_2b_{21}}{(b_{21}x_1+b_{22}x_2+1)^2} & \frac{(1+r_2)(1-c_2)(b_{21}x_1+1)}{(b_{21}x_1+b_{22}x_2+1)^2} + c_2 \end{pmatrix}$$

obviously has nonnegative diagonal entries and nonpositive off-diagonal entries, i.e. (iii) in Lemma 4.1 holds. By Remark 2, one has $\det DT(x) > 0$ for all $x \in \mathbb{R}_+^2$ and T is injective, so (ii) and (iv) in Lemma 4.1 hold. Now the conclusion follows from Lemma 4.1. \square

Besides the trivial fixed point 0, the map T has two axial fixed points $q_{\{1\}} = (r_1/b_{11}, 0)$, $q_{\{2\}} = (0, r_2/b_{22})$. The fixed point $q_{\{i\}}$ is just the intersection of the line $S_i = \{x \in \mathbb{R}_+^2 : b_{ii}x_i + b_{ij}x_j = r_i, i \neq j\}$ and the x_i -coordinate axis. If S_1 and S_2 intersect in \mathbb{R}_+^2 , then there also exists a positive fixed point p at the intersection of S_1 and S_2 .

Let U_i and B_i be the unbounded and bounded connected components of $\mathbb{R}_+^2 \setminus S_i$, respectively. Let $\gamma_{ij} := r_j - b_{ji}\frac{r_i}{b_{ii}}$ for $i, j = 1, 2$ and $i \neq j$. Then $q_{\{i\}} \in U_j$ if and only if $\gamma_{ij} < 0$ and $q_{\{i\}} \in B_j$ if and only if $\gamma_{ij} > 0$.

Lemma 4.2. *If $\gamma_{ij} > 0$ (resp. < 0), then $q_{\{i\}}$ is a saddle (resp. an asymptotically stable node), and hence repels (resp. attracts) on Σ . Moreover, $q_{\{i\}}$ is hyperbolic if and only if $\gamma_{ij} \neq 0$.*

Proof. We prove this for $q_{\{1\}}$. The eigenvalues of the Jacobian matrix

$$DT(q_{\{1\}}) = \begin{pmatrix} \frac{c_1r_1+1}{1+r_1} & -\frac{(1-c_1)r_1b_{12}}{(1+r_1)b_{11}} \\ 0 & \frac{(1+r_2)(1-c_2)b_{11}}{b_{21}r_1+b_{11}} + c_2 \end{pmatrix}$$

are $\frac{c_1r_1+1}{1+r_1}$, $\frac{(1+r_2)(1-c_2)b_{11}}{b_{21}r_1+b_{11}} + c_2$. They are both positive. Note that $0 < \frac{c_1r_1+1}{1+r_1} < 1$ and the coordinate axis x_1 is invariant, so every orbit originating from the positive

x_1 -axis tends to $q_{\{1\}}$. If $\frac{(1+r_2)(1-c_2)b_{11}}{b_{21}r_1+b_{11}} + c_2 > 1$ (resp. < 1), i.e., if $\gamma_{12} > 0$ (resp. < 0), then $q_{\{1\}}$ is a saddle (resp. an asymptotically stable node), and hence repels (resp. attracts) on Σ . The last statement is obvious. \square

Remark 4. Recall that $\gamma_{ij} > 0$ (resp. < 0) if and only if $q_{\{i\}} \in B_j$ (resp. U_j). So the nature of the fixed point $q_{\{i\}}$ can be determined by the position of $q_{\{i\}}$ relative to the line S_j , $i \neq j$. Moreover, if $\gamma_{12}\gamma_{21} > 0$ (resp. < 0), then S_1 and S_2 intersect (resp. do not intersect) in \mathbb{R}_+^2 , i.e., there exists (resp. does not exist) a positive fixed point p .

The following theorem is an immediate consequence of Proposition 2, Lemma 4.2 and Remark 4. The analysis in [31] carries over to the present situation in a straightforward way.

Theorem 4.3. *Let $T \in \text{CGAA}(2)$.*

- (a) *If $\gamma_{12} < 0, \gamma_{21} > 0$, then the positive fixed point p does not exist and $q_{\{1\}}$ attracts all points not on the x_2 -axis.*
- (b) *If $\gamma_{12} > 0, \gamma_{21} < 0$, then the positive fixed point p does not exist and $q_{\{2\}}$ attracts all points not on the x_1 -axis.*
- (c) *If $\gamma_{12}, \gamma_{21} > 0$, then T has a hyperbolic positive fixed point p attracting all points in \mathbb{R}_+^2 .*
- (d) *If $\gamma_{12}, \gamma_{21} < 0$, then T has a positive fixed point p which is a hyperbolic saddle. Moreover, every nontrivial orbit tends to one of the asymptotically stable nodes $q_{\{1\}}$ or $q_{\{2\}}$ or to the saddle p .*

Remark 5. The statements of Theorem 4.3 have clear biological interpretations, which we present here.

- (i) If $\gamma_{ij} > 0$, then species j can invade species i while it cannot invade if $\gamma_{ij} < 0$.
- (ii) If species j can invade species i but not vice versa, then species i is driven to extinction, whilst species j remains extant.
- (iii) In the case of mutual invadability, that is, if both species can invade the other, then there will be coexistence in the form of an asymptotically stable positive fixed point.
- (iv) If neither species can invade (mutual noninvadability), there is no coexistence: one of the species will oust the other. The surviving species depends on the initial conditions. (Convergence to the positive saddle happens only for initial conditions in a set of measure zero and is hence impossible in nature).

The situations mentioned above are of particular interest when the two populations 1 and 2 are not different species, but different traits (resident and mutant) of the same species. To begin with, the resident ($i = 1$) is at the fixed point $q_{\{1\}}$ and then the mutant $q_{\{2\}}$ is introduced in small quantities. Case (i) $\gamma_{12} > 0$ gives the condition for successful invasion. Case (ii) describes trait substitution. Case (iii) is an example of protected dimorphism. For a discussion of these notions and their consequences for evolutionary dynamics we refer the reader to [14, 15, 17, 18].

The following definition of equivalence appears to be unnecessarily pompous, but it prepares the way for the analogous definition in higher dimensions. Let $T, \hat{T} \in \text{CGAA}(2)$. T and \hat{T} are said to be *equivalent relative to $\partial\Sigma$* if there exists a permutation σ of $\{1, 2\}$ such that T has a fixed point $q_{\{i\}}$ if and only if \hat{T} has a fixed point $\hat{q}_{\{\sigma(i)\}}$, and further $q_{\{i\}}$ has the the same hyperbolicity and local dynamics as $\hat{q}_{\{\sigma(i)\}}$. A model $T \in \text{CGAA}(2)$ is said to be *stable relative to $\partial\Sigma$* if all the

fixed points on $\partial\Sigma$ are hyperbolic. We say that an equivalence class is *stable* if each mapping in it is stable relative to $\partial\Sigma$.

Corollary 2. *There are a total of 3 stable equivalence classes in $\text{CGAA}(2)$. The three dynamical scenarios are presented in Fig. 1.*



FIGURE 1. The dynamics in Σ replaced by Δ^1 . A closed dot \bullet stands for a fixed point attracting on Σ , and an open dot \circ stands for the one repelling on Σ . Each Σ denotes an equivalence class.

Remark 6. Suppose that $T \in \text{CGAA}(2)$ is stable relative to $\partial\Sigma$ and possesses a positive fixed point p . Then $\det B \neq 0$, the positive fixed point p is unique and given by

$$p = \left(\frac{b_{22}\gamma_{21}}{\det B}, \frac{b_{11}\gamma_{12}}{\det B} \right).$$

It follows from the positivity of p that γ_{12} and γ_{21} both have the same sign as $\det B$. Hence, by Theorem 4.3 (c) and (d), p attracts on Σ if and only if $\det B > 0$ and repels on Σ if and only if $\det B < 0$.

Biologically, $\det B > 0$ means that both species can invade, while $\det B < 0$ means that none of them can (Remark 5 (i)).

4.2. Classification of the 3-dimensional maps. We are now ready to analyze the three-dimensional model (14). We let S_i be the plane $\{x \in \mathbb{R}_+^3 : b_{ii}x_i + b_{ij}x_j + b_{ik}x_k = r_i, i \neq j \neq k\}$ and U_i and B_i be the unbounded and bounded connected components of $\mathbb{R}_+^3 \setminus S_i$, respectively.

Recall that $q_{\{1\}} = (r_1/b_{11}, 0, 0)$, $q_{\{2\}} = (0, r_2/b_{22}, 0)$, $q_{\{3\}} = (0, 0, r_3/b_{33})$ are the three axial fixed points of T . If S_i, S_j meet in the interior of π_k , then T has a fixed point $v_{\{k\}}$. T admits a positive fixed point p if and only if S_i, S_j and S_k intersect in \mathbb{R}_+^3 . Let

$$\gamma_{ij} := r_j - b_{ji} \frac{r_i}{b_{ii}}, \quad \beta_{ij} = \frac{r_i b_{jj} - r_j b_{ij}}{b_{ii} b_{jj} - b_{ij} b_{ji}} \quad (16)$$

for $i, j = 1, 2, 3$ and $i \neq j$.

Let $T, \hat{T} \in \text{CGAA}(3)$. T and \hat{T} are said to be *equivalent relative to $\partial\Sigma$* if there exists a permutation σ of $\{1, 2, 3\}$ such that T has a fixed point $q_{\{i\}}$ (or $v_{\{k\}}$) if and only if \hat{T} has a fixed point $\hat{q}_{\{\sigma(i)\}}$ (or $\hat{v}_{\{\sigma(k)\}}$), and further $q_{\{i\}}$ (or $v_{\{k\}}$) has the same hyperbolicity and local dynamics as $\hat{q}_{\{\sigma(i)\}}$ (or $\hat{v}_{\{\sigma(k)\}}$). A map $T \in \text{CGAA}(3)$ is said to be *stable relative to $\partial\Sigma$* if all the fixed points on $\partial\Sigma$ are hyperbolic. We call an equivalence class *stable* if each map in it is stable relative to $\partial\Sigma$.

By the invariance of π_i and the analysis of the 2-dimensional case in §4.1, the classification program, statements, proofs in [31] carry over to $\text{CGAA}(3)$ in a straightforward way, so we do not need to re-do it.

Lemma 4.4. *If $\gamma_{ij} > 0$ (resp. < 0) then $q_{\{i\}}$ repels (resp. attracts) on $\partial\Sigma \cap \pi_k$, where i, j, k are distinct. Furthermore, if $\gamma_{ij}, \gamma_{ik} > 0$ (resp. < 0) then the fixed point $q_{\{i\}}$ is a repeller (resp. an attractor) on Σ ; if $\gamma_{ij}\gamma_{ik} < 0$, then the fixed point $q_{\{i\}}$ is a saddle on Σ ; and $q_{\{i\}}$ is hyperbolic if and only if $\gamma_{ij}\gamma_{ik} \neq 0$.*

Lemma 4.5. *If $\gamma_{jk}\gamma_{kj} > 0$ then T admits a fixed point $v_{\{i\}}$ in the interior of π_i , where i, j, k are distinct. Moreover, if $\gamma_{jk}, \gamma_{kj} < 0$ (resp. > 0) then $v_{\{i\}}$ repels (resp. attracts) along $\partial\Sigma$.*

The biological meaning of the condition $\gamma_{ij} > 0$ (resp. < 0) in Lemmas 4.4-4.5 is that species j can (resp. not) invade species i in the absence of species k ; here i, j, k are distinct.

Lemma 4.6. *Suppose that the planar fixed point $v_{\{i\}}$ exists. Then $(Bv_{\{i\}}^\tau)_i < r_i$ (resp. $> r_i$) implies that $v_{\{i\}}$ locally repels (resp. attracts) in $\dot{\Sigma}$. Moreover, $v_{\{i\}}$ is hyperbolic if and only if $(Bv_{\{i\}}^\tau)_i \neq r_i$.*

Remark 7. It is easy to check that $(Bv_{\{k\}}^\tau)_k < r_k$ (resp. $> r_k$) if and only if $b_{ki}\beta_{ij} + b_{kj}\beta_{ji} < r_k$ (resp. $> r_k$). A model $T \in \text{CGAA}(3)$ is stable relative to $\partial\Sigma$ if and only if $\gamma_{ij} \neq 0$ and $b_{ki}\beta_{ij} + b_{kj}\beta_{ji} \neq r_k$, i.e., $(Bv_{\{k\}}^\tau)_k \neq r_k$ (if $v_{\{k\}}$ exists). Suppose that T is stable relative to $\partial\Sigma$. If T admits a positive fixed point p satisfying (12), then p is the unique positive fixed point. Otherwise, assume that T has two different positive fixed points p and \tilde{p} . Now $p_s := sp + (1-s)\tilde{p}$ is a solution of (12) for any $s \geq 0$. Let $\bar{s} := \sup\{s > 0 : p_s \in \Sigma\}$. Then $p_{\bar{s}} \in \partial\Sigma$ is a fixed point, which is not hyperbolic, contradicting that T is stable relative to $\partial\Sigma$. Therefore, B^{-1} exists so 1 is not an eigenvalue of $DT(p)$.

Proposition 3. *Suppose that $T \in \text{CGAA}(3)$ is stable relative to $\partial\Sigma$. Then we have the formula*

$$\sum_{i=1}^3 (\mathcal{J}(q_{\{i\}}, T) + 2\mathcal{J}(v_{\{i\}}, T)) + 4\mathcal{J}(p, T) = 1. \quad (17)$$

Proposition 4. *Assume that $T \in \text{CGAA}(3)$ is stable relative to $\partial\Sigma$. Then we have $\mathcal{J}(q_{\{i\}}, T) = 1$ (resp. $\mathcal{J}(v_{\{i\}}, T) = 1$) if $q_{\{i\}}$ (resp. $v_{\{i\}}$) is a repeller or an attractor on Σ and $\mathcal{J}(q_{\{i\}}, T) = -1$ (resp. $\mathcal{J}(v_{\{i\}}, T) = -1$) if $q_{\{i\}}$ (resp. $v_{\{i\}}$) is a saddle on Σ . Moreover, $\mathcal{J}(p, T) = 0$ if and only if p does not exist.*

Theorem 4.7. *There are a total of 33 stable equivalence classes in $\text{CGAA}(3)$.*

Proof. It is a straightforward combinatorial task to classify the stable equivalence classes, which is based on the index formula (17), Remark 7 and a geometric analysis of the positions of the three planes S_j .

- Step 1 There are a total of 2^6 possibilities for the non-zero values of $\text{sgn}(r_{ij})$ which reduce to 16 possibilities modulo permutation of the indices.
- Step 2 Under the given values of $\text{sgn}(r_{ij})$ one can determine the existence of the fixed points $v_{\{k\}}$. Then applying formula (17) to each of the 16 possibilities obtained in Step 1, we count 57 possibilities for the indices of all the fixed points on the corresponding Σ , which reduce to 45 possibilities modulo permutation of the indices.
- Step 3 By the positions of S_1, S_2, S_3 for each of the 45 cases, 12 nonexistent cases can be ruled out. Then we derive the total of 33 stable equivalence classes.

□

The corresponding parameter conditions and the dynamics in Σ for each of the 33 stable classes are listed in Table 1. Any model stable relative to $\partial\Sigma$ in $\text{CGAA}(3)$ is in one of the 33 classes (modulo permutation of the indices). Eighteen classes (classes 1 – 18) do not possess the positive fixed point p and it is proved in §4.3

that every orbit of these models converges to a fixed point on $\partial\Sigma$. The other 15 classes with a positive fixed point p may have relatively complex dynamics, e.g. Neimark-Sacker bifurcations, Chenciner bifurcations, or heteroclinic cycles.

4.3. Dynamics on the carrying simplex. As befits the context, we shall consider the families of models given in Table 1 by permutation of the indices, i.e., we assume the parameters b_{ij}, r_i, c_i of the corresponding class satisfy the conditions listed in the table.

Recalling §3.1, each map $T \in \text{CGAA}(3)$ satisfies A1)-A2) in Theorem 3.1, which implies that $G_i(y) < G_i(x)$ for all $i \in N$ provided $x < y$, and T is competitive and one-to-one on \mathbb{R}_+^3 , so conditions C1)-C3) of Theorem 2.2 in [42] hold for T . By Remark 7, each map $T \in \text{CGAA}(3)$ which is stable relative to $\partial\Sigma$ has only finitely many fixed points, so it satisfies C4) of Theorem 2.2 in [42]. Then by Theorem 2.2 in [42] we conclude the following result.

Lemma 4.8. *Suppose that $T \in \text{CGAA}(3)$ is stable relative to $\partial\Sigma$. If T has no positive fixed point, then every nontrivial orbit converges to some fixed point on $\partial\Sigma$.*

According to the index formula (17) and Proposition 4, one has $\mathcal{J}(p, T) = 0$ for each map T in the stable classes 1 – 18, so there is no positive fixed point for these maps. The following proposition follows from Lemma 4.8 immediately.

Proposition 5. *For each map T in classes 1 – 18, every nontrivial orbit converges to some fixed point on $\partial\Sigma$.*

From a biological point of view, Proposition 5 means that if there is no coexistence, then some of the species will be extinct.

Now we only need to study classes 19 – 33. Note that each model in them has a unique positive fixed point $p = (p_1, p_2, p_3)$. We will focus on analyzing whether these classes can admit Neimark-Sacker bifurcations and Chenciner bifurcations (for a textbook treatment of these two bifurcations, see [36]). These bifurcations can bifurcate invariant closed curves, which either consist of periodic points or are quasiperiodic curves. Moreover, at Chenciner bifurcations two isolated invariant closed curves can be created. We prove that classes 19 – 25 can not admit these two bifurcations, while classes 26 – 31 can admit Neimark-Sacker bifurcations. We also construct examples to show that classes 26 – 29 can admit Chenciner bifurcations numerically by using the methods provided in [19], so in these classes, there may exist two invariant closed curves.

Lemma 4.9. *For each map in classes 19–25, we have $\mathcal{J}(p, T) = -1$ and $\det B < 0$; while for each map in classes 26 – 33, we have $\mathcal{J}(p, T) = 1$ and $\det B > 0$.*

Proof. For classes 19 – 25 (resp. classes 26 – 33), it follows from the local dynamics of fixed points on $\partial\Sigma$ in Table 1 and formula (17) directly that $\mathcal{J}(p, T) = -1$ (resp. $\mathcal{J}(p, T) = 1$). Moreover, if $\mathcal{J}(p, T) = -1$, then all the three eigenvalues of $DT(p)$ are positive real numbers with one eigenvalue greater than 1 and the other two less than 1 by Remark 3. So, two eigenvalues of $\text{diag}[p_i \frac{1-c_i}{1+r_i}]B$ are greater than 0 and one is less than 0, which implies that $\det B < 0$. While $\mathcal{J}(p, T) = 1$ ensures that there are zero or two eigenvalues of $DT(p)$ greater than 1 by Remark 3. For the former case, also by Remark 3 we have one eigenvalue of $\text{diag}[p_i \frac{1-c_i}{1+r_i}]B$ is greater than 0 and the other two are either complex numbers or greater than 0. For the latter case, two eigenvalues of $\text{diag}[p_i \frac{1-c_i}{1+r_i}]B$ are less than 0 and one is greater than 0. Therefore, $\det B > 0$. \square

Proposition 6. *The positive fixed point p is always a saddle on Σ in classes 19–25, and hence these classes can not admit Neimark-Sacker bifurcations or Chenciner bifurcations.*

Proof. By Lemma 4.9 one has that $\mathcal{J}(p, T) = -1$ and all the three eigenvalues of $DT(p)$ are positive real numbers with one eigenvalue greater than 1 and the other two less than 1. Since Σ is invariant and transverse to all strictly positive vectors, the local dynamics of p on Σ is reflected by the other two eigenvalues except λ^* , where $0 < \lambda^* < 1$ is defined in Remark 3. Thus, p is a saddle on Σ . Since one necessary condition for Neimark-Sacker bifurcations and Chenciner bifurcations occurring at p is that $DT(p)$ has a pair of complex conjugate eigenvalues of modulus 1, these bifurcations can not occur in these classes. \square

Lemma 4.10 (Proposition 3.8 in [52]). *Let $M = (m_{ij})_{n \times n}$ be an $n \times n$ matrix. If $\det M_{\{i,j\}} < 0$ for each principal 2×2 submatrix $M_{\{i,j\}} = \begin{pmatrix} m_{ii} & m_{ij} \\ m_{ji} & m_{jj} \end{pmatrix}$, $i < j$, then M has an eigenvalue with negative real part.*

Proposition 7. *The positive fixed point p is always a repeller on Σ in class 32, and hence this class can not admit Neimark-Sacker bifurcations or Chenciner bifurcations.*

Proof. Note that each map T in class 32 admits a fixed point $v_{\{k\}}$ repelling along $\partial\Sigma \cap \pi_k$ for any $k = 1, 2, 3$ (see Table 1 (32)), so $v_{\{k\}}$ is a saddle for $T|_{\pi_k}$. Thus $\det B_{\{i,j\}} < 0$ ($i < j$) by Remark 6, and hence $\det M_{\{i,j\}} < 0$, where $M = \text{diag}[p_i \frac{1-c_i}{1+r_i}]B$. By $\det B > 0$, one has $\det M > 0$. Then it follows from Lemma 4.10 and $\det M > 0$ that M has two eigenvalues with negative real parts. Therefore, $DT(p) = I - M$ has two eigenvalues with real parts greater than 1, i.e., $DT(p)$ has two eigenvalues with magnitudes greater than 1 except λ^* . Recall that the local dynamics of p on Σ is reflected by the other two eigenvalues except λ^* , so p is a repeller on Σ and hence Neimark-Sacker bifurcations and Chenciner bifurcations do not occur within this class. \square

Proposition 8. *For each map T from any of classes 26–33, there exists a map $\hat{T} \in \text{CGAA}(3)$ in the same class with the positive fixed point $\hat{p} = (1, 1, 1)$ topologically equivalent to T .*

Proof. Set $z_i(k) = x_i(k)/p_i$, $i = 1, 2, 3$, where $\{x(k) : k \in \mathbb{Z}_+\}$ is the positive trajectory emanating from $x(0) = (x_1, x_2, x_3)$ for T . Then

$$\begin{aligned} z_i(k+1) &= x_i(k+1)/p_i \\ &= \frac{1}{p_i} \left(\frac{(1+r_i)(1-c_i)x_i(k)}{1+\sum_{j=1}^3 b_{ij}x_j(k)} + c_i x_i(k) \right) \\ &= \frac{(1+r_i)(1-c_i)z_i(k)}{1+\sum_{j=1}^3 b_{ij}p_j z_j(k)} + c_i z_i(k) \\ &= \frac{(1+r_i)(1-c_i)z_i(k)}{1+(B \text{diag}[p_j](z(k))^\tau)_i} + c_i z_i(k) \\ &:= \frac{(1+r_i)(1-c_i)z_i(k)}{1+(\hat{B}z(k))^\tau_i} + c_i z_i(k), \end{aligned}$$

where $\hat{B} = B \text{diag}[p_i]$. Hence $\{z(k) : k \in \mathbb{Z}_+\}$ is the positive trajectory emanating from $z(0) = (x_1/p_1, x_2/p_2, x_3/p_3)$ for $\hat{T} = (\hat{T}_1, \hat{T}_2, \hat{T}_3) \in \text{CGAA}(3)$ with $\hat{T}_i(z) := \frac{(1+r_i)(1-c_i)z_i}{1+(\hat{B}z)^\tau_i} + c_i z_i$, $i = 1, 2, 3$. It follows from $(Bp^\tau)_i = r_i$ that $(\hat{B}\hat{p}^\tau)_i = r_i$, where

$\hat{p} = (1, 1, 1)$, i.e., $(1, 1, 1)$ is a positive fixed point of \hat{T} . It is clear that \hat{T} and T are topologically equivalent and also equivalent relative to $\partial\Sigma$. \square

By Proposition 8, we may assume that the fixed point p of T from any of the stable classes 26 – 33 is at $(1, 1, 1)$. Then the parameters b_{ij}, r_i of T satisfy that $\sum_j b_{ij} = r_i$, $i = 1, 2, 3$, i.e., the sum of the i th row of $B = (b_{ij})_{3 \times 3}$ is r_i . Besides, $DT(p) = I - \text{diag}[\frac{1-c_i}{1+r_i}]B$. Hereafter, we always assume that $n = 3$, and $b_{ij}, r_i > 0$ satisfying $\det B > 0$ and $\sum_j b_{ij} = r_i$, $i = 1, 2, 3$. Consider the map $T \in \text{CGAA}(3)$ with the parameters b_{ij}, r_i, c_i , where $0 < c_i < 1$. Let $A := I - \text{diag}[\frac{1-c_i}{1+r_i}]B$.

Lemma 4.11. *Under the above assumptions, we have*

- (a) *if $\det B_{\{i,j\}} < 0$, then for $0 < c_k < 1$ sufficiently close to 1, the matrix A has two eigenvalues with magnitudes greater than 1, where i, j, k are distinct;*
- (b) *if $\det B_{\{i,j\}} > 0$, then for $0 < c_k < 1$ sufficiently close to 1, the matrix A has two eigenvalues with magnitudes less than 1, where i, j, k are distinct.*

Proof. Set $M := \text{diag}[\frac{1-c_i}{1+r_i}]B$. Then for definiteness, let $i = 1, j = 2, k = 3$.

(a) By $\det B_{\{1,2\}} < 0$, one has $\det M_{\{1,2\}} < 0$. For $c_3 = 1$, the entries in the third row of M are 0, so M has a negative eigenvalue and a positive eigenvalue besides 0. Since the eigenvalues of M depend continuously on c_3 , thus for $0 < c_3 < 1$ sufficiently close to 1, M has an eigenvalue with negative real part. Recall that $\det B > 0$, so $\det M > 0$, which implies that M has two eigenvalues with negative real parts. Therefore, A has two eigenvalues with real parts greater than 1, i.e., A has two eigenvalues with magnitudes greater than 1.

(b) By $\det B_{\{1,2\}} > 0$, one has $\det M_{\{1,2\}} > 0$. So, M has two positive eigenvalues besides 0 for $c_3 = 1$ because $M_{\{1,2\}}$ is a positive matrix. It follows from $r_i = b_{i1} + b_{i2} + b_{i3}$ that the sum of each row of M is less than 1. Then the Perron-Frobenius theorem ensures that both of the two positive eigenvalues are less than 1. Thus A has two eigenvalues with magnitudes less than 1 for $c_3 = 1$, and hence for $0 < c_3 < 1$ sufficiently close to 1. \square

Lemma 4.12. *Under the above assumptions, if $\det B_{\{i,j\}}$, $i < j$, are not all of the same sign (i.e., at least one is positive and one is negative), then there exist $0 < c_i < 1$, $i = 1, 2, 3$ such that A possesses a pair of complex conjugate eigenvalues of modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$, where i stands for the imaginary unit.*

Proof. Without loss of generality, assume that $\det B_{\{1,2\}} > 0, \det B_{\{1,3\}} < 0$. First fix $0 < c_1 < 1$, $0 < c_2 = \mu_0 < 1$. Since $\det B_{\{1,2\}} > 0$, it follows from Lemma 4.11 that there exists $0 < c_3 = \mu_3 < 1$ sufficiently close to 1 such that A has two eigenvalues with magnitudes less than 1. Now fix c_1 and $c_3 = \mu_3$. Since $\det B_{\{1,3\}} < 0$, Lemma 4.11 ensures that A has two eigenvalues with magnitudes greater than 1 for $0 < c_2 = \mu_1 < 1$ sufficiently close to 1. Thus, as c_2 varies from μ_0 to μ_1 , at least one of the eigenvalues of A varies continuously from having magnitude less than 1 to magnitude greater than 1, and necessarily crosses the unit circle in the complex plane. Since $\det B \neq 0$, 1 is not an eigenvalue of A . On the other hand, by Remark 3 one knows that all the eigenvalues of A have positive real parts. So $-1, \pm i, (-1 \pm \sqrt{3}i)/2$ are not eigenvalues of A ; and moreover, there exists a $0 < \mu_2 < 1$ such that A has a pair of complex conjugate eigenvalues of modulus 1 as $c_2 = \mu_2$. Now one can choose $c_1, c_2 = \mu_2, c_3 = \mu_3$. \square

Given $b_{ij}, r_i > 0, 0 < c_1, c_3 < 1$ such that $\det B > 0$ and $\sum_{j=1}^3 b_{ij} = r_i$, $i, j = 1, 2, 3$. Let $\hat{B} = \text{diag}[\frac{1-c_1}{1+r_1}, 1, \frac{1-c_3}{1+r_3}]B := (\hat{b}_{ij})_{3 \times 3}$, $0 < c_2 = s < 1$, and $M^s = \text{diag}[1, \psi(s), 1]\hat{B}$, where $\psi(s) = \frac{1-s}{1+r_2}$. Denote by $f(z, s) = \det(M^s - zI)$ the characteristic polynomial of M^s . Let $A^s = I - M^s$. Assume that A^s has a pair of complex conjugate eigenvalues of modulus 1 at $0 < s = s_0 < 1$ which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. Now for any s in a small neighborhood V of s_0 , A^s has a pair of complex conjugate eigenvalues $w(s), \overline{w(s)}$ with $|w(s_0)| = 1$. We let $w(s) = u(s) + iv(s)$ for $s \in V$.

Lemma 4.13. *Under the above assumptions, $\frac{d|w(s)|}{ds}|_{s=s_0} \neq 0$.*

Proof. Noticing that

$$\begin{aligned} \text{tr}(M^s) &= \hat{b}_{11} + \psi(s)\hat{b}_{22} + \hat{b}_{33}, \\ \det M_{\{1,2\}}^s &= \psi(s) \det \hat{B}_{\{1,2\}}, \\ \det M_{\{1,3\}}^s &= \det \hat{B}_{\{1,3\}}, \\ \det M_{\{2,3\}}^s &= \psi(s) \det \hat{B}_{\{2,3\}}, \\ \det M^s &= \psi(s) \det \hat{B}, \end{aligned}$$

the proof is a copy of that of Lemma 4.14 in [32] by replacing $\frac{s}{c_2(s)}$ to be $\psi(s)$. \square

Let $c = (c_1, c_2, c_3)$ with $0 < c_i < 1$, $i = 1, 2, 3$.

Theorem 4.14. *Given $b_{ij}, r_i > 0$ such that $\det B > 0$ and $\sum_{j=1}^3 b_{ij} = r_i$, $i, j = 1, 2, 3$. Consider the map $T^c \in \text{CGAA}(3)$ given by (14) with the parameters $b_{ij}, r_i > 0$ and $0 < c_i < 1$. If $\det B_{\{i,j\}}$, $i < j$, $i, j = 1, 2, 3$, are not all of the same sign, then there exists some $\hat{c} = (\hat{c}_1, \hat{c}_2, \hat{c}_3)$ with $0 < \hat{c}_i < 1$ such that the Jacobian matrix $DT^{\hat{c}}(p)$ has a pair of complex conjugate eigenvalues $\lambda_{1,2}^{\hat{c}}$ with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$, where $p = (1, 1, 1)$ is the positive fixed point. Furthermore, the restriction of T^c to the two dimensional center manifold at the critical parameter value \hat{c} can be transformed to the complex Poincaré normal form*

$$\omega \mapsto (1 + \beta)e^{i\theta(\beta)}\omega + d(\beta)\omega|\omega|^2 + O(|\omega|^4), \quad \omega \in \mathbb{C}, \quad (18)$$

where ω is a complex variable and $d(\beta)$ is a complex function.

Proof. Let $A^c := DT^c(p) = I - \text{diag}[\frac{1-c_1}{1+r_1}]B$. It follows from Lemma 4.12 that there exist $0 < \hat{c}_i < 1$, $i = 1, 2, 3$ such that $A^{\hat{c}}$ has a pair of complex conjugate eigenvalues $\lambda_{1,2}^{\hat{c}}$ with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$.

Fix $c_1 = \hat{c}_1$ and $c_3 = \hat{c}_3$. Set $c_2 = s$, and write $A^s := A^c$. Let $s_0 = \hat{c}_2$. Then A^s admits a pair of complex conjugate eigenvalues with modulus 1 at $0 < s = s_0 < 1$. Thus A^s has a pair of complex conjugate eigenvalues $w(s), \overline{w(s)}$ with $|w(s_0)| = 1$ for s in a small neighborhood V of s_0 . By Lemma 4.13, one has $\frac{d|w(s)|}{ds}|_{s=s_0} \neq 0$. Then the conclusion follows from [36, Theorem 4.5], which can be proved in quite the same manner as the Theorem 4.3 in [32] (see also [37]), so we omit it. \square

Let $L_1(0) := \text{Re}(e^{-i\theta(0)}d(0))$, which is the first Lyapunov coefficient (see [37]). Using Theorem 4.14 and [36, Theorem 4.6], we have the following result.

Theorem 4.15. *Let the hypotheses of Theorem 4.14 hold. If $L_1(0) \neq 0$, then the family of maps $\{T^c : 0 < c_i < 1, i = 1, 2, 3\}$ admits a Neimark-Sacker bifurcation. Moreover, if $L_1(0) < 0$, a stable invariant closed curve bifurcates from the fixed*

point p while an unstable invariant closed curve bifurcates from the fixed point p if $L_1(0) > 0$.

It should be pointed out that the conditions $\lambda_{1,2}^{\hat{c}} \neq \pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$, the possible roots of $z^k = 1$ for $k = 1, 2, 3, 4$, in Theorems 4.14-4.15 are not merely technical; see [36, Chapter 4]. If they are not satisfied, the invariant closed curve may not appear at all, or other complex dynamics might occur; see [36, Chapter 9] and [37] for more details. However, for $T \in \text{CGAA}(3)$ in the stable classes 26 – 33, Remark 3 ensures that $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$ can not be the eigenvalues of $DT(p)$.

The biological interpretation of the condition $\det B_{\{i,j\}} < 0$ in Lemmas 4.11-4.12 and Theorems 4.14-4.15 is that at most one of the species i and j can invade the other in the absence of species k , whilst $\det B_{\{i,j\}} > 0$ means that at least one of the species i and j can invade the other in the absence of species k . Therefore, the biological meaning of the condition $\det B_{\{i,j\}}, i < j$, being not all of the same sign (say $\det B_{\{i,j\}} < 0$ and $\det B_{\{i,k\}} > 0$) is that at most one of the species i and j can invade the other in the absence of species k , whilst at least one of the species i and k can invade the other in the absence of species j .

Proposition 9. *Neimark-Sacker bifurcations can occur within each of classes 26 – 31.*

Proof. Note that there exist mappings in each of classes 26 – 31 satisfying the hypotheses of Theorem 4.15, so by Theorem 4.15 one can obtain the result immediately. See Example 4.1 for definiteness. \square

Example 4.1. Let

$$B^{[26]} = \begin{pmatrix} 2 & 1 & 1 \\ 1 & 1 & 6 \\ 4 & 2 & 6 \end{pmatrix}, B^{[27]} = \begin{pmatrix} 1 & 1 & \frac{1}{3} \\ 1 & 1 & \frac{8}{3} \\ 4 & 1 & 2 \end{pmatrix}, B^{[28]} = \begin{pmatrix} \frac{7}{3} & 4 & \frac{1}{6} \\ 7 & 4 & 2 \\ 14 & 4 & \frac{3}{2} \end{pmatrix},$$

$$B^{[29]} = \begin{pmatrix} 119 & \frac{73}{2} & 7 \\ \frac{357}{2} & 146 & \frac{1}{2} \\ \frac{119}{4} & \frac{1825}{4} & \frac{3}{2} \end{pmatrix}, B^{[30]} = \begin{pmatrix} 1 & 21 & 2 \\ 3 & 21 & 24 \\ 6 & 42 & 24 \end{pmatrix}, B^{[31]} = \begin{pmatrix} \frac{9}{2} & 1 & 4 \\ \frac{9}{2} & 12 & \frac{5}{2} \\ 9 & 12 & \frac{15}{2} \end{pmatrix},$$

and $r_j^{[i]} = (B^{[i]}p^\tau)_j$, where $p = (1, 1, 1)$, $i = 26, \dots, 31$ and $j = 1, 2, 3$. Consider the map $T^{[i,c]} \in \text{CGAA}(3)$ with the parameters $B^{[i]}$, $r_j^{[i]}$ and $0 < c_j < 1$. It is easy to check that $T^{[i,c]}$ belongs to class i , and $\det B_{\{j,k\}}^{[i]}$, $j < k$, are not all of the same sign for $i = 26, \dots, 31$. Furthermore, we have the following results by Theorem 4.15.

1. Set $i = 26$. Let $c_1 = s$, $c_2 = c_3 = 1/2$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. It is not difficult to check that for $s = \frac{16969}{12782} - \frac{\sqrt{44373169}}{12782}$, $DT^{[i,c]}(p)$ has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. Furthermore, by calculating we obtain the first Lyapunov coefficient $L_1(0) = -2.204 \times 10^{-3} < 0$. Since the Lyapunov coefficient is a rather lengthy expression, the approximate value was computed as a *rational* by using MATLAB [19, 37]. Thus, by Theorem 4.15 there is a supercritical Neimark-Sacker bifurcation in class 26, i.e., a stable invariant closed curve bifurcates from the fixed point p .

2. Set $i = 27$. Let $c_2 = s$, $c_1 = c_3 = 1/2$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. As $s = \frac{338071}{109489} - \frac{68\sqrt{12476689}}{109489}$, $DT^{[i,c]}(p)$

has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. The first Lyapunov coefficient is $L_1(0) = -2.51 \times 10^{-3} < 0$. So, class 27 can admit supercritical Neimark-Sacker bifurcations, i.e., there may exist stable invariant closed curves in this class.

3. For $i = 28$, we let $c_2 = s$, $c_1 = c_3 = 1/2$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. When $s = \frac{2830237}{2128872} - \frac{7\sqrt{10910811109}}{2128872}$, $DT^{[i,c]}(p)$ has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. The first Lyapunov coefficient $L_1(0) = -1.028 \times 10^{-5} < 0$. Thus, by Theorem 4.15 there is a supercritical Neimark-Sacker bifurcation in class 28, i.e., a stable invariant closed curve bifurcates from the fixed point p .

4. For $i = 29$, we let $c_2 = s$, $c_1 = 1/10$, $c_3 = 1/5$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. When $s = \frac{1047914923699693}{518308301564745} - \frac{4\sqrt{703723890988454819368257121}}{103661660312949}$, $DT^{[i,c]}(p)$ has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. The first Lyapunov coefficient $L_1(0) = -4.279 \times 10^{-6} < 0$. So, class 29 can admit supercritical Neimark-Sacker bifurcations, i.e., there may exist stable invariant closed curves in this class.

5. For $i = 30$, we set $c_2 = s$, $c_1 = c_3 = 1/2$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. As $s = \frac{349187}{291720} - \frac{\sqrt{3847272361}}{291720}$, $DT^{[i,c]}(p)$ has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. The first Lyapunov coefficient $L_1(0) = 7.092 \times 10^{-4} > 0$. So, class 30 can admit subcritical Neimark-Sacker bifurcations, i.e., there may exist unstable invariant closed curves in this class.

6. For $i = 31$, we set $c_2 = s$, $c_1 = c_3 = 1/2$, and $c = (c_1, c_2, c_3)$. Consider the family of maps $\{T^{[i,c]} : 0 < c_j < 1, j = 1, 2, 3\}$. As $s = \frac{36280753}{26310573} - \frac{40\sqrt{65857329493}}{26310573}$, $DT^{[i,c]}(p)$ has a pair of complex conjugate eigenvalues with modulus 1 which do not equal $\pm 1, \pm i, (-1 \pm \sqrt{3}i)/2$. The first Lyapunov coefficient $L_1(0) = -1.27 \times 10^{-3} < 0$. By Theorem 4.15 we know that there is a supercritical Neimark-Sacker bifurcation in class 31, i.e., a stable invariant closed curve bifurcates from the fixed point p .

Some numerical experiments are also done to show that some models in classes 26, 27, 29 and 31 possess attracting quasiperiodic curves, that is the invariant closed curves are quasiperiodic curves in these models. See Figs. 2-5.

Remark 8. For the 3-dimensional standard Atkinson-Allen model (3), it is shown that classes 26 and 27 can admit Neimark-Sacker bifurcations while classes 28, 30 and 32 can not (see [31]). For the 3-dimensional generalized Atkinson-Allen model (4), we have shown that classes 26 – 31 can admit Neimark-Sacker bifurcations. Thus one can see that this is a significant difference between model (3) and model (4), and the generalized Atkinson-Allen model (4) contains much richer dynamics. Furthermore, we will give some numerical examples to show that classes 26 – 29 for model (4) can also admit Chenciner bifurcations, which means that in these classes, two isolated invariant closed curves may coexist.

Consider a sufficiently smooth map $\Phi(x, \beta) : \mathbb{R}^n \times \mathbb{R}^2 \rightarrow \mathbb{R}^n$, where $x \in \mathbb{R}^n, \beta \in \mathbb{R}^2$. Assume that Φ has a fixed point $x = 0$ at $\beta = 0$ for which the Neimark-Sacker bifurcation conditions hold. Thus $D\Phi(0, 0)$ has a pair of conjugate complex eigenvalues lying on the unit circle. Assume further that Φ satisfies some other non-degeneracy conditions such that the restriction of Φ to the two dimensional center manifold at the critical parameter value $\beta = 0$ can be transformed to the

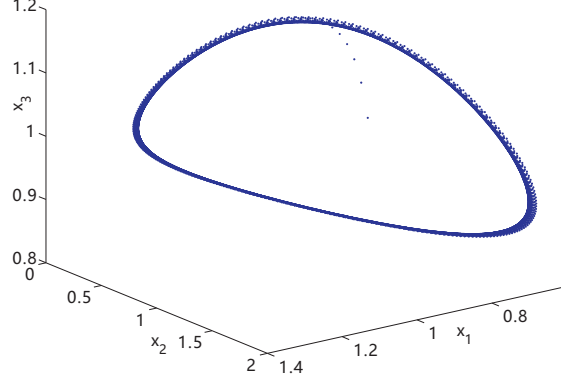


FIGURE 2. The orbit emanating from $x_0 = (0.7667, 0.7667, 1)$ for the map $T \in \text{CGAA}(3)$ with the parameters $B^{[26]}$, $r_i^{[26]}$ and c_i , $i = 1, 2, 3$ tends to an attracting quasiperiodic curve (the blue circle), where $B^{[26]}$ and $r_i^{[26]}$ are given in Example 4.1 and $c_1 = 0.81, c_2 = 0.5, c_3 = 0.5$.

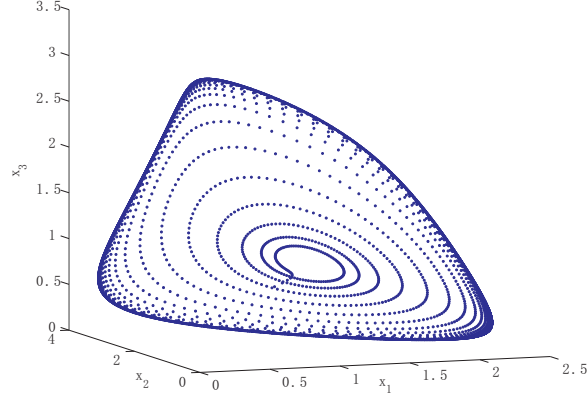


FIGURE 3. The orbit emanating from $x_0 = (0.7667, 1, 0.7667)$ for the map $T \in \text{CGAA}(3)$ with the parameters $B^{[27]}$, $r_i^{[27]}$ and c_i , $i = 1, 2, 3$ tends to an attracting quasiperiodic curve (the blue boundary), where $B^{[27]}$ and $r_i^{[27]}$ are given in Example 4.1 and $c_1 = 0.2, c_2 = 0.8, c_3 = 0.8$.

normal form in polar coordinates (ϱ, θ) (see [36] for more details):

$$\begin{cases} \varrho \mapsto \varrho + \mu_1 \varrho + \mu_2 \varrho^3 + L_2(\mu) \varrho^5 + \cdots, \\ \theta \mapsto \theta + \vartheta(\mu) + v(\mu, \varrho) \varrho^2 + \cdots, \end{cases}$$

where $\mu = (\mu_1, \mu_2)$ and the dots denote terms of higher order in ϱ and θ . Truncating the higher order terms gives the map

$$\begin{cases} \varrho \mapsto \varrho + \mu_1 \varrho + \mu_2 \varrho^3 + L_2(\mu) \varrho^5, \\ \theta \mapsto \theta + \vartheta(\mu) + v(\mu, \varrho) \varrho^2. \end{cases} \quad (19)$$

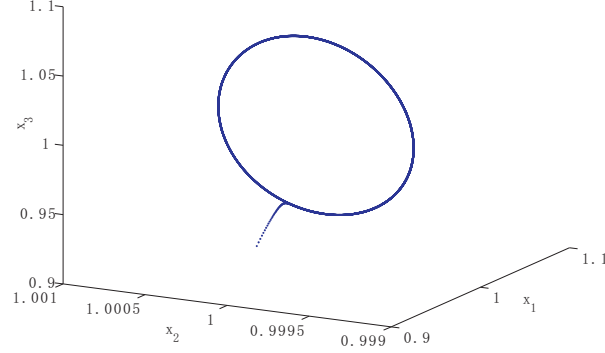


FIGURE 4. The orbit emanating from $x_0 = (0.9333, 1, 0.9333)$ for the map $T \in \text{CGAA}(3)$ with the parameters $B^{[29]}$, $r_i^{[29]}$ and c_i , $i = 1, 2, 3$ tends to an attracting quasiperiodic curve (the blue circle), where $B^{[29]}, r_i^{[29]}$, $i = 1, 2, 3$ are given in Example 4.1 and $c_1 = 0.89, c_2 = 0.9995, c_3 = 0.8$.

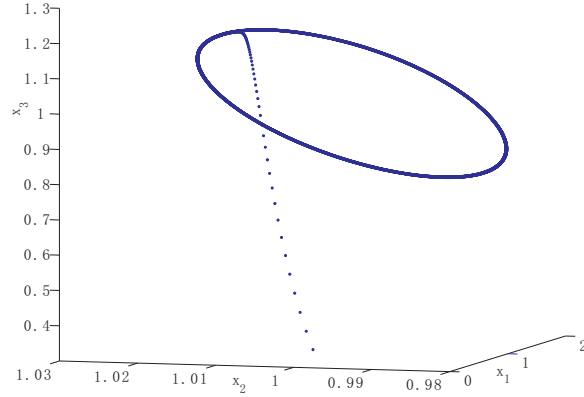


FIGURE 5. The orbit emanating from $x_0 = (0.3333, 1, 0.3333)$ for the map $T \in \text{CGAA}(3)$ with the parameters $B^{[31]}$, $r_i^{[31]}$ and c_i , $i = 1, 2, 3$ tends to an attracting quasiperiodic curve (the blue circle), where $B^{[31]}, r_i^{[31]}$ are given in Example 4.1 and $c_1 = 0.9, c_2 = 0.9962, c_3 = 0.75$.

$\varrho = 0$ corresponds to the fixed point of the system and any positive fixed point of the ϱ -map in (19) corresponds to an invariant closed curve in phase space. $\mu_1 = 0$ corresponds to the Neimark-Sacker bifurcation curve, for which a pair of conjugate complex eigenvalues lie on the unit circle, and μ_2 is the corresponding first Lyapunov coefficient when $\mu_1 = 0$. For $\mu_2 < 0$, a supercritical Neimark-Sacker bifurcation occurs at $\mu_1 = 0$, whereas for $\mu_2 > 0$ a subcritical Neimark-Sacker bifurcation occurs at $\mu_1 = 0$. For $\mu_2 = 0$ the Neimark-Sacker bifurcation becomes degenerate,

which is called the Chenciner bifurcation (see [36, 13]). The Chenciner bifurcation occurs at $\mu = 0$ for which a pair of conjugate complex eigenvalues lie on the unit circle and the first Lyapunov coefficient $\mu_2 = 0$. An extra non-degeneracy condition for the Chenciner bifurcation is $L_2(0) \neq 0$. Here we show some details by assuming that $L_2(0) < 0$. Without loss of generality, we assume that $L_2(0) = -1$.

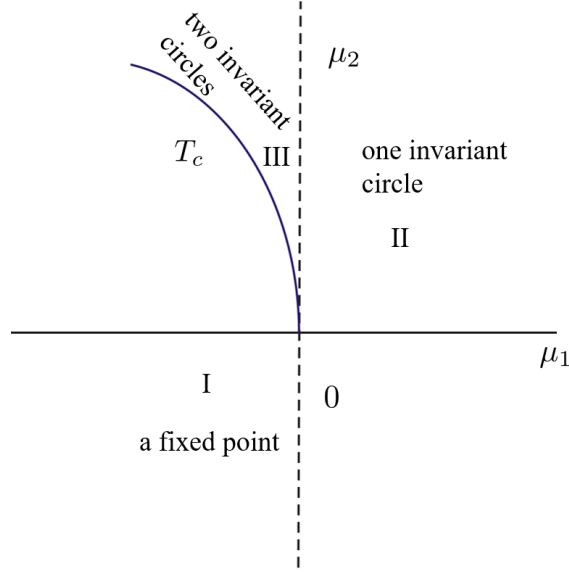


FIGURE 6. Bifurcation diagram of the Chenciner bifurcation in the (μ_1, μ_2) -plane for the case $L_2(0) < 0$. The origin is the Chenciner bifurcation point. The vertical dashed line $\mu_1 = 0$ is the Neimark-Sacker bifurcation curve. In the region I below the curve T_c , there is only one fixed point which is stable; in the region II ($\mu_1 > 0$), there is a unique invariant closed curve which is stable; in the region III between the curve T_c and the positive μ_2 -axis, a stable invariant closed curve (outer) and an unstable invariant closed curve (inner) coexist; on the solid curve T_c , these two circles coincide.

ϱ^* is positive fixed point of the ϱ -map in (19) if and only if it is a positive solution to the equation $\mu_1 + \mu_2 \varrho^2 - \varrho^4 = 0$, i.e.,

$$\left(\varrho^2 - \frac{\mu_2}{2}\right)^2 = \frac{\mu_2^2}{4} + \mu_1. \quad (20)$$

When $\mu_1 > 0$ there is exactly one positive solution for equation (20). For $\mu_1 < 0$, equation (20) has no solution when $\frac{\mu_2^2}{4} + \mu_1 < 0$, while equation (20) has two distinct positive solutions when $\frac{\mu_2^2}{4} + \mu_1 > 0$, $\mu_1 < 0$ and $\mu_2 > 0$ (in this case, the outer invariant closed curve is stable, while the inner one is unstable). For μ lying on the curve $T_c := \{\mu : \frac{\mu_2^2}{4} + \mu_1 = 0, \mu_2 > 0\}$, equation (20) has two equal positive solutions (in this case, the unstable and stable invariant closed curves approach each other). See Fig. 6 for a sketch of this bifurcation diagram. For $L_2(0) > 0$, it can be treated similarly, and in this case, the outer invariant closed curve is unstable, while the inner one is stable.

The Chenciner bifurcation is a two-parameter bifurcation phenomenon of a fixed point. Although the normal form computations for Chenciner bifurcations are straightforward, in practical models they can be very complicated. Here based on the numerical methods provided in [19], we do numerical experiments by using MATLAB [37, 20] to show that classes 26 – 29 can admit Chenciner bifurcations, so in these classes, there may exist two invariant closed curves. See Example 4.2.

Example 4.2. Consider the parameters $B^{[i]}, r_j^{[i]}$ given in Example 4.1, where $i = 26, 27, 28, 29$, and $j = 1, 2, 3$.

1. Set $i = 26$. Let $c_3 = 0.5$, $0 < c_1, c_2 < 1$, and $c = (c_1, c_2, c_3)$. By numerical calculation, we find that the two-parameter model $T^{[i, c]}$ with the coefficients $B^{[i]}, r_j^{[i]}$ and c has a Chenciner bifurcation point at $p = (1, 1, 1)$ when $c_1 = 0.901467$ and $c_2 = 0.756706$. The normal form coefficient $L_2(0) = 3.285 \times 10^{-4} > 0$, so a large unstable invariant closed curve surrounding a small stable invariant closed curve can occur in class 26. Numerical simulations show that for appropriate parameters (c_1, c_2) in the vicinity of the critical values, say $c_1 = 0.901436, c_2 = 0.75661$, the orbit for the model $T^{[i, c]}$ with such parameters emanating from the point near the positive fixed point tends to a stable invariant closed curve while the orbit emanating from the point away from the positive fixed point tends to the axial fixed point $q_{\{2\}} = (0, 8, 0)$. For example, the orbit starting from $x_0 = (1.001, 1.002, 1.001)$ tends to a stable invariant closed curve while the orbit starting from $x_0 = (1.13, 1.05, 1.01)$ tends to $q_{\{2\}}$. This inspires us to conjecture that the phase portrait of this map $T^{[i, c]}$ on its carrying simplex has the structure as shown in Fig. 7.

2. Set $i = 27$. Let $c_3 = 0.5$, $0 < c_1, c_2 < 1$, and $c = (c_1, c_2, c_3)$. The two-parameter

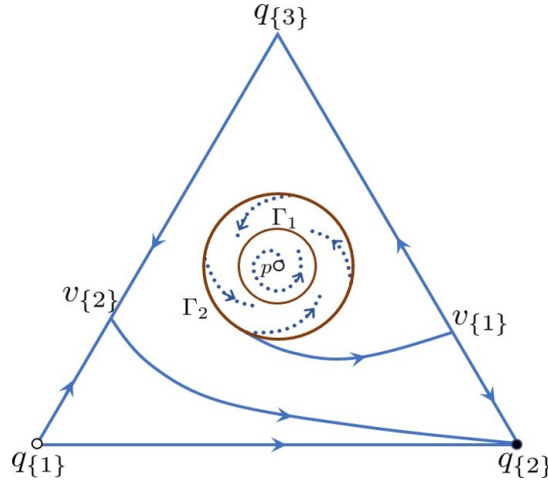


FIGURE 7. A possible phase portrait on the carrying simplex for the map $T \in \text{CGAA}(3)$ in class 26. A stable invariant closed curve, the smaller red circle Γ_1 , and an unstable invariant closed curve, the bigger red circle Γ_2 coexist. All the orbits in $\dot{\Sigma} \setminus (\Gamma_2 \cup R_p(\Gamma_2))$ except those on the stable manifold restricted to Σ of $v_{\{1\}}$ converge to the axial fixed point $q_{\{2\}}$, where $R_p(\Gamma_2)$ denotes the component of $\Sigma \setminus \Gamma_2$ containing p .

model $T^{[i, c]}$ with the coefficients $B^{[i]}, r_j^{[i]}$ and c has a Chenciner bifurcation point

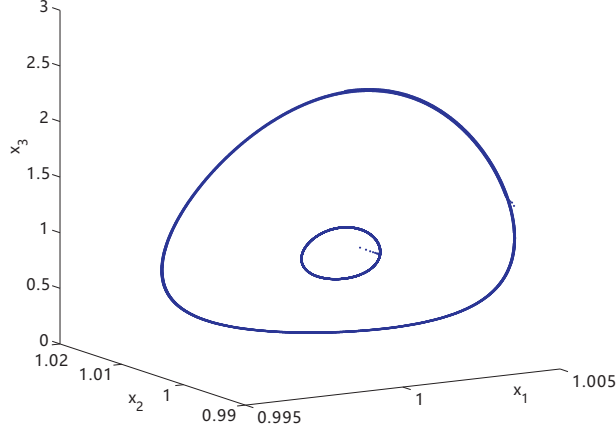


FIGURE 8. The orbits emanating from $x_0 = (1.004, 0.9927, 1.48)$ and $x_0 = (1.001, 1.002, 1.001)$ for the map $T \in \text{CGAA}(3)$ with the parameters $B^{[29]}$, $r_i^{[29]}$ and $c_1 = 0.999655$, $c_2 = 0.339655$, $c_3 = 0.2$ are asymptotic to the bigger quasiperiodic curve and the smaller one respectively, where $B^{[29]}$ and $r_i^{[29]}$ are given in Example 4.1.

at $p = (1, 1, 1)$ when $c_1 = 0.858323$ and $c_2 = 0.939276$. The normal form coefficient $L_2(0) = -6.493 \times 10^{-4} < 0$, so a stable fixed point and an attracting (large) invariant closed curve, separated by an unstable invariant closed curve can coexist in class 27.

3. Set $i = 28$. Let $c_3 = 0.5$, $0 < c_1, c_2 < 1$, and $c = (c_1, c_2, c_3)$. The two-parameter model $T^{[i, c]}$ with the coefficients $B^{[i]}$, $r_j^{[i]}$ and c has a Chenciner bifurcation point at $p = (1, 1, 1)$ when $c_1 = 0.524555$ and $c_2 = 0.986162$. The normal form coefficient $L_2(0) = 1.025 \times 10^{-4} > 0$, so an unstable fixed point and an unstable (large) invariant closed curve, separated by a stable invariant closed curve can coexist in class 28.

4. Set $i = 29$. Let $c_3 = 0.2$, $0 < c_1, c_2 < 1$, and $c = (c_1, c_2, c_3)$. The two-parameter model $T^{[i, c]}$ with the coefficients $B^{[i]}$, $r_j^{[i]}$ and c has a Chenciner bifurcation point at $p = (1, 1, 1)$ when $c_1 = 0.999655$ and $c_2 = 0.338655$. The normal form coefficient $L_2(0) = 7.157 \times 10^{-8} > 0$, so class 29 can admit two invariant closed curves, a large unstable invariant closed curve, and a small stable invariant closed curve. Fig. 8 shows that the model $T^{[i, c]}$ with the parameters $c_1 = 0.999655$, $c_2 = 0.339655$ near the critical values admits two attracting invariant closed curves on its carrying simplex simultaneously, where the orbits emanating from $x_0 = (1.004, 0.9927, 1.48)$ and $x_0 = (1.001, 1.002, 1.001)$ tend to a bigger attracting quasiperiodic curve and a smaller one respectively.

We now turn to study another interesting phenomenon, the occurrence of heteroclinic cycles. Suppose that the 3-dimensional map T has a carrying simplex Σ , which is homeomorphic to Δ^2 . Suppose further that $q_{\{1\}} = (q_1, 0, 0)$, $q_{\{2\}} = (0, q_2, 0)$ and $q_{\{3\}} = (0, 0, q_3)$ are its three axial fixed points lying on the vertices of Σ . If each $q_{\{i\}}$ is a saddle, and $\partial\Sigma \cap \pi_i$ is the heteroclinic connection between $q_{\{j\}}$ and $q_{\{k\}}$, then T admits a heteroclinic cycle of May-Leonard type: $q_{\{1\}} \rightarrow q_{\{2\}} \rightarrow q_{\{3\}} \rightarrow q_{\{1\}}$ (or

the arrows reserved), which is just the boundary of Σ . We refer the readers to [33] for more details and the stability of such heteroclinic cycles.

Lemma 4.16 (Theorem 3 in [33]). *Suppose that $\partial\Sigma$ is a heteroclinic cycle above. Then the heteroclinic cycle $\partial\Sigma$ repels (attracts) if*

$$\prod_{i=1}^3 \ln G_i(q_{\{i-1\}}) + \prod_{i=1}^3 \ln G_i(q_{\{i+1\}}) > 0 \text{ } (< 0),$$

where $i \in \{1, 2, 3\}$ is considered cyclic.

Note that for any map T in class 27, each axial fixed point $q_{\{i\}}$ is a saddle on Σ , and $\partial\Sigma \cap \pi_i$ is the heteroclinic connection between $q_{\{j\}}$ and $q_{\{k\}}$, where i, j, k are distinct. So $\partial\Sigma$ forms a heteroclinic cycle of May-Leonard type: $q_{\{1\}} \rightarrow q_{\{2\}} \rightarrow q_{\{3\}} \rightarrow q_{\{1\}}$ (or the arrows reserved), i.e., any map T in class 27 possesses a heteroclinic cycle (see Table 1 (27)). By Lemma 4.16 one can obtain Proposition 10 immediately.

Set $\nu_{ij} = \frac{(1+r_j)(1-c_j)b_{ii}}{b_{ii}+b_{ji}r_i} + c_j$, where $i \neq j$. Let

$$\vartheta = \ln \nu_{12} \ln \nu_{23} \ln \nu_{31} + \ln \nu_{21} \ln \nu_{13} \ln \nu_{32}.$$

Proposition 10. *Assume that $T \in \text{CGAA}(3)$ is in class 27. If $\vartheta < 0$ (> 0), then the heteroclinic cycle $\partial\Sigma$ of T attracts (repels).*

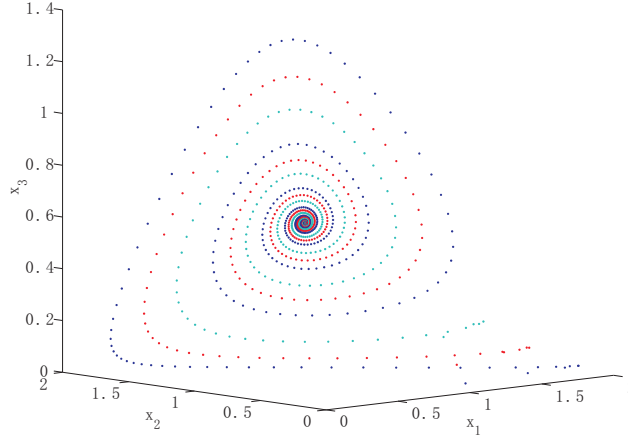


FIGURE 9. The orbits emanating from $x_0 = (1, 0.0333, 0.0333)$, $x_0 = (1, 0.1, 0.1)$ and $x_0 = (1, 0.2, 0.2)$ for the map $T \in \text{CGAA}(3)$ in Example 4.3 lead away from $\partial\Sigma$ and tend to the positive fixed point p .

Example 4.3. Let $B = \begin{pmatrix} 1 & \frac{5}{4} & \frac{1}{2} \\ \frac{1}{2} & 1 & \frac{5}{4} \\ \frac{5}{4} & \frac{1}{2} & 1 \end{pmatrix}$, $c_1 = 0.1, c_2 = 0.2, c_3 = 0.1$, and $r_1 =$

$2.1, r_2 = 2, r_3 = 1.9$. Consider the map $T \in \text{CGAA}(3)$ with the parameters B, c_i and $r_i, i = 1, 2, 3$. It is easy to check that T belongs to class 27 with $\vartheta > 0$. It then

follows from Proposition 10 that the heteroclinic cycle $\partial\Sigma$ repels for T and see also the numerical experiment in Fig. 9.

Let $\hat{B} = \begin{pmatrix} 2 & 4 & 1 \\ 1 & 2 & 4 \\ 4 & 1 & 2 \end{pmatrix}$, $\hat{c}_1 = 0.2, \hat{c}_2 = 0.1, \hat{c}_3 = 0.1$, and $\hat{r}_1 = 1.9, \hat{r}_2 = 2, \hat{r}_3 =$

2.1. Consider the map $\hat{T} \in \text{CGAA}(3)$ with the parameters \hat{B} , \hat{c}_i and \hat{r}_i , $i = 1, 2, 3$. It is easy to check that \hat{T} belongs to class 27 with $\vartheta < 0$. It then follows from Proposition 10 that the heteroclinic cycle $\partial\Sigma$ attracts for \hat{T} and see also the numerical experiment in Fig. 10.

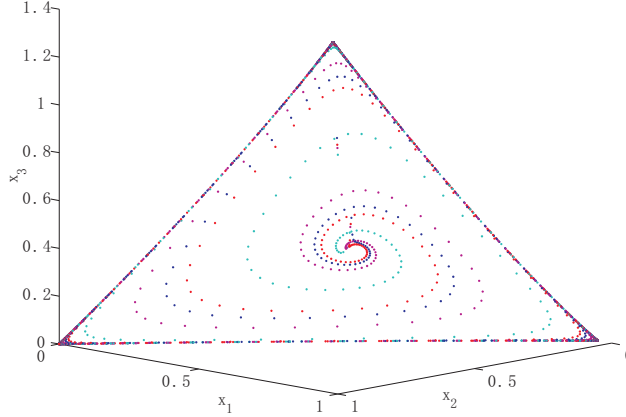


FIGURE 10. The orbits emanating from $x_0 = (0.8333, 0.8333, 1)$, $x_0 = (0.9, 0.9, 1)$ and $x_0 = (0.9333, 0.9333, 1)$ for the map $\hat{T} \in \text{CGAA}(3)$ in Example 4.3 approach to $\partial\Sigma$.

Remark 9. Note that for the class 33, the hypotheses in Theorem 4.15 do not hold, so whether this class admits a Neimark-Sacker bifurcation or a Chenciner bifurcation is open.

5. Comparison with LV systems. In this section, we use some numerical examples to show that the 3-dimensional generalized Atkinson-Allen model (14) is not dynamically consistent with the continuous-time competitive LV system

$$\frac{dx_i(t)}{dt} = x_i(t)(\nu_i - \sum_{j=1}^3 \mu_{ij}x_j(t)), \quad \nu_i, \mu_{ij} > 0, i, j = 1, 2, 3, \quad (21)$$

where $\nu_i = (1 - c_i)r_i$, $\mu_{ij} = (1 - c_i)b_{ij}$, and $0 < c_i < 1$, though it also acts as a discrete-time Lotka-Volterra system (see Section 1). Certainly, model (14) and system (21) have the same steady states.

Consider the LV system (21) with the parameters $B^{[26]}$, $r_i^{[26]}$, $i = 1, 2, 3$ given in Example 4.1 and $c_1 = 0.81, c_2 = 0.5, c_3 = 0.5$. The coexistence steady state $p = (1, 1, 1)$ is unstable for (14) and (21). Fig. 2 shows that the orbit emanating from $x_0 = (0.7667, 0.7667, 1)$ for model (14) with these parameters tends to an attracting quasiperiodic curve, while Fig. 11 shows that the orbit emanating from x_0 converges to the axial steady state $q_{\{2\}} = (0, 8, 0)$ for system (21).

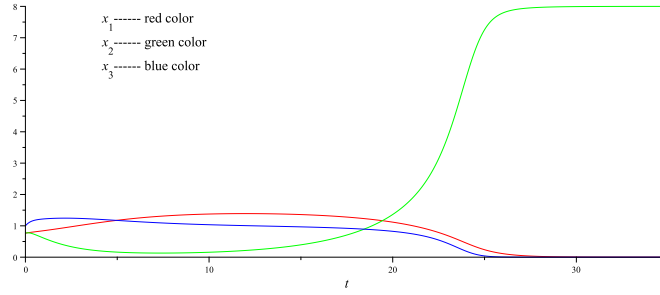


FIGURE 11. The orbit emanating from $x_0 = (0.7667, 0.7667, 1)$ converges to the axial steady state $q_{\{2\}} = (0, 8, 0)$ for system (21).

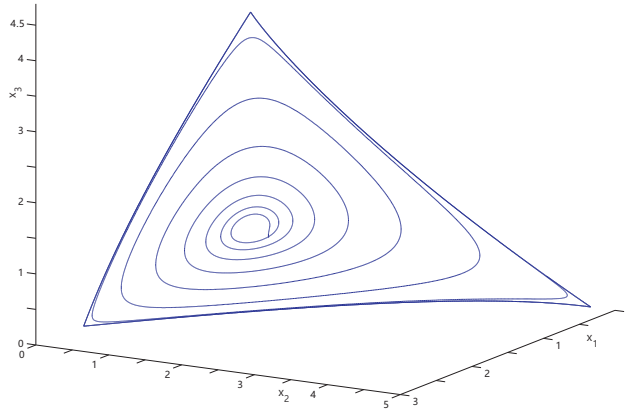


FIGURE 12. The orbit emanating from $x_0 = (0.7667, 1, 0.7667)$ approaches the heteroclinic cycle for system (21).

Consider the LV system (21) with the parameters $B^{[27]}$, $r_i^{[27]}$, $i = 1, 2, 3$ given in Example 4.1 and $c_1 = 0.2, c_2 = 0.8, c_3 = 0.8$. The coexistence steady state $p = (1, 1, 1)$ is unstable for (14) and (21). Both of the two systems have a heteroclinic cycle as the boundaries of their carrying simplices. The heteroclinic cycle for model (14) is repelling by Proposition 10, while the one is attracting for system (21) by [27]. Moreover, Fig. 3 shows that the orbit emanating from $x_0 = (0.7667, 1, 0.7667)$ for model (14) with these parameters tends to an attracting quasiperiodic curve, while Fig. 12 shows that the orbit emanating from x_0 approaches the heteroclinic cycle for system (21).

Consider the LV system (21) with the parameters $B^{[31]}$, $r_i^{[31]}$, $i = 1, 2, 3$ given in Example 4.1 and $c_1 = 0.9, c_2 = 0.9962, c_3 = 0.75$. The coexistence steady state $p = (1, 1, 1)$ is unstable for (14) while stable for LV system (21). Moreover, Fig. 5 shows that the orbit emanating from $x_0 = (0.3333, 1, 0.3333)$ for model (14) with these parameters tends to an attracting quasiperiodic curve, while Fig. 13 shows that the orbit emanating from x_0 converges to p for system (21).

The 3-dimensional generalized Atkinson-Allen model (14) and the LV system (21) also have consistent dynamics. Consider the LV system (21) with the parameters B , c_i and r_i , $i = 1, 2, 3$ given in Example 4.3. Both of the two systems have an

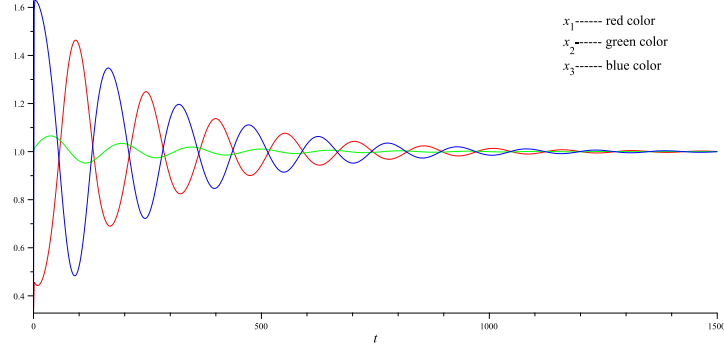


FIGURE 13. The orbit emanating from $x_0 = (0.3333, 1, 0.3333)$ tends to $p = (1, 1, 1)$ for LV system (21).

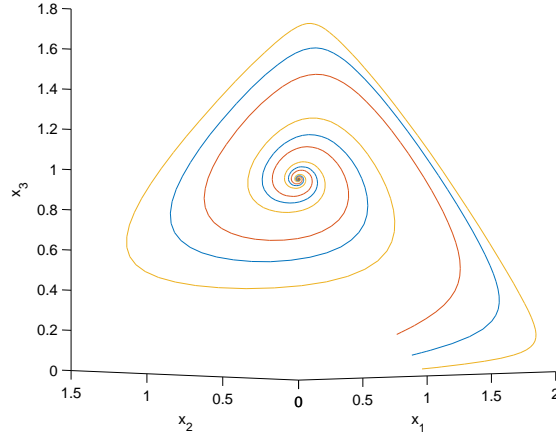


FIGURE 14. The orbits emanating from $x_0 = (1, 0.0333, 0.0333)$, $x_0 = (1, 0.1, 0.1)$ and $x_0 = (1, 0.2, 0.2)$ for LV system (21) with the parameters B , c_i and r_i given in Example 4.3 tend to $p = (\frac{258}{385}, \frac{346}{385}, \frac{236}{385})$.

attracting coexistence steady state $p = (\frac{258}{385}, \frac{346}{385}, \frac{236}{385})$ and a repelling heteroclinic cycle. The orbits emanating from $x_0 = (1, 0.0333, 0.0333)$, $x_0 = (1, 0.1, 0.1)$ and $x_0 = (1, 0.2, 0.2)$ for model (14) and LV system (21) tend to p ; see Figs. 9 and 14.

Consider the LV system (21) with the parameters \hat{B} , \hat{c}_i and \hat{r}_i , $i = 1, 2, 3$ given in Example 4.3. Both of the two systems have a repelling coexistence steady state $p = (\frac{11}{35}, \frac{17}{70}, \frac{3}{10})$ and an attracting heteroclinic cycle. The orbits emanating from $x_0 = (0.8333, 0.8333, 1)$, $x_0 = (0.9, 0.9, 1)$ and $x_0 = (0.9333, 0.9333, 1)$ for model (14) and LV system (21) approach their heteroclinic cycles respectively; see Figs. 10 and 15.

6. Discussion. This paper proves that any n -dimensional generalized Atkinson-Allen map $T \in \text{CGAA}(n)$ can possess a carrying simplex Σ . Based on the existence of Σ , we define an equivalence on the set $\text{CGAA}(3)$, i.e., two mappings in $\text{CGAA}(3)$

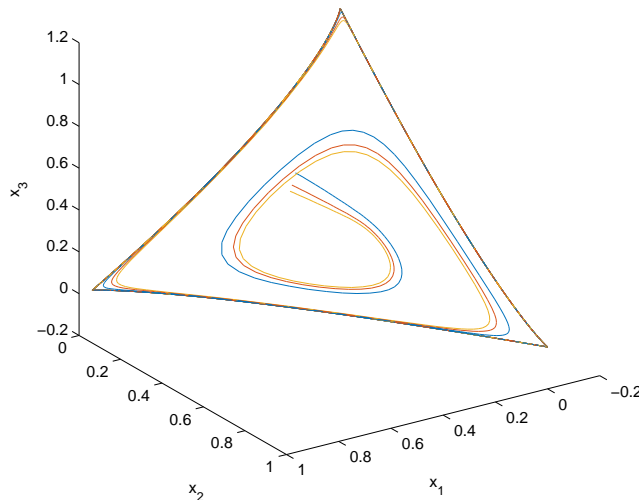


FIGURE 15. The orbits emanating from $x_0 = (0.8333, 0.8333, 1)$, $x_0 = (0.9, 0.9, 1)$ and $x_0 = (0.9333, 0.9333, 1)$ for LV system (21) with parameters \hat{B} , \hat{c}_i and \hat{r}_i given in Example 4.3 approach to the heteroclinic cycle.

are said to be equivalent if all the boundary fixed points have the same local dynamics on the carrying simplices after a permutation of the indices $\{1, 2, 3\}$. Then using the index formula for fixed points on Σ , we derive a total of 33 stable equivalence classes for CGAA(3) via combinatorial technique.

The dynamics of each map from any of classes 1 – 18 is trivial, i.e., every nontrivial trajectory converges to some fixed point on $\partial\Sigma$ and the global dynamics of these maps can be determined by the local dynamics of fixed points on $\partial\Sigma$. However, the dynamics of those maps from classes 19 – 33 are relatively complex which may not be determined by the local dynamics of fixed points on $\partial\Sigma$ only. In classes 19 – 25, each map has a positive fixed point which is a saddle on Σ , so within each of these classes Neimark-Sacker bifurcations and Chenciner bifurcations can not occur. See Table 1 (19)-(25). Within each of classes 26 – 31, there do exist Neimark-Sacker bifurcations, which means that invariant closed curves can occur in these classes. Numerical experiments show that the three-dimensional generalized Atkinson-Allen model possesses asymptotically attracting isolated quasiperiodic curves, and also show that classes 26 – 29 can admit Chenciner bifurcations, i.e., these classes can possess two isolated invariant closed curves. Our examples show that a larger unstable invariant closed curve surrounding a smaller stable invariant closed curve can occur on Σ in classes 26, 28 and 29, while a larger stable invariant closed curve surrounding a smaller unstable invariant closed curve can occur on Σ in class 27. Neimark-Sacker bifurcations and Chenciner bifurcations do not occur in class 32, while whether there is a Neimark-Sacker bifurcation or Chenciner bifurcation in class 33 or not is open.

Another interesting phenomenon is that each map in class 27 possesses a heteroclinic cycle, i.e. a cyclic arrangement of saddle fixed points and heteroclinic connections. The competition coefficients in this class can be seen to correspond to the biological environment where in purely pairwise competition 1 beats 2, 2 beats 3, and 3 beats 1. It is this intransitivity in the pairwise competition which leads to such cyclic behavior. We further provide the criteria on the stability of heteroclinic cycles, and also show that this model indeed admits heteroclinic cycle attractors, i.e. under mild conditions the model in class 27 exhibits a general class of orbits which cycle from being composed almost wholly of species 1, to almost wholly 2, to almost wholly 3, back to almost wholly 1 etc. Our classification makes it possible to investigate much more various interesting dynamics within each of classes 19 – 33.

Recall that for the standard 3-dimensional Atkinson-Allen model (3), classes 28 and 30 can not admit Neimark-Sacker bifurcations, while for the generalized Atkinson-Allen model $T \in \text{CGAA}(3)$, each of classes 26 – 31 can admit Neimark-Sacker bifurcations, and classes 26 – 29 can admit Chenciner bifurcations, so the generalized Atkinson-Allen model contains much richer dynamics. The generalized Atkinson-Allen model is also not dynamically consistent with the continuous-time competitive Lotka-Volterra system.

However, it is worth noting that several problems remain open. We propose some as follows.

- Unlike the continuous-time systems, for which the Poincaré-Bendixson theorem holds, how to obtain the global dynamics of classes 19 – 25 for the discrete-time 3-dimensional generalized Atkinson-Allen model is open.
- Enlightened by Figs. 7 and 8, it is extremely interesting to provide criteria to guarantee that the 3-dimensional generalized Atkinson-Allen model has multiple invariant closed curves in classes 26 – 33. So far there have been many results on the coexistence of multiple limit cycles for 3-dimensional competitive Lotka-Volterra equations ([22, 23, 24, 28, 34, 38, 47, 48]).
- Whether the generalized Atkinson-Allen model can possess a center on Σ or not is also unknown.
- Give sufficient conditions to guarantee that the positive fixed point is globally attracting on Σ . Recently, we learn that Baigent provides a sufficient condition to guarantee the global stability of the positive fixed point for the 3-dimensional Leslie-Gower model and Ricker model respectively [3].

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Appendix A. Appendix: The stable equivalence classes in $\text{CGAA}(3)$.

Table 1: The 33 equivalence classes in CGAA(3), where

$$\gamma_{ij} := r_j - b_{ji} \frac{r_i}{b_{ii}}, \beta_{ij} = \frac{r_i b_{jj} - r_j b_{ij}}{b_{ii} b_{jj} - b_{ij} b_{ji}}$$

for $i, j = 1, 2, 3$ and $i \neq j$, and each Σ is given by a representative model of that class. A fixed point is represented by a closed dot \bullet if it attracts on Σ , by an open dot \circ if it repels on Σ , and by the intersection of its hyperbolic manifolds if it is a saddle on Σ .

Class	The Corresponding Parameters	Phase Portrait in Σ
1	$\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} < 0$	
2	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
3	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$	
4	(i) $\gamma_{12} > 0, \gamma_{13} < 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
5	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
6	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$	
7	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
8	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	

Table 1: (continued)

Class	The Corresponding Parameters	Phase Portrait in Σ
9	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
10	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
11	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 < 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
12	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 < 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
13	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} > 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
14	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
15	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
16	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	

Table 1: (continued)

Class	The Corresponding Parameters	Phase Portrait in Σ
17	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 > 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
18	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 > 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
19	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$	
20	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
21	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 < 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
22	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 > 0$	
23	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
24	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
25	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 > 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	

Table 1: (continued)

Class	The Corresponding Parameters	Phase Portrait in Σ
26	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 < 0$	
27	$\gamma_{12} > 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} < 0$	
28	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
29	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
30	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} > 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
31	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} < 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	
32	(i) $\gamma_{12} < 0, \gamma_{13} < 0, \gamma_{21} < 0, \gamma_{23} < 0, \gamma_{31} < 0, \gamma_{32} < 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 > 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 > 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 > 0$	
33	(i) $\gamma_{12} > 0, \gamma_{13} > 0, \gamma_{21} > 0, \gamma_{23} > 0, \gamma_{31} > 0, \gamma_{32} > 0$ (ii) $b_{12}\beta_{23} + b_{13}\beta_{32} - r_1 < 0$ (iii) $b_{21}\beta_{13} + b_{23}\beta_{31} - r_2 < 0$ (iv) $b_{31}\beta_{12} + b_{32}\beta_{21} - r_3 < 0$	

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